TAXONOMY AND PHYLOGENY OF THE ROVE BEETLE GENUS *PHLAEOPTERUS* (COLEOPTERA: STAPHYLINIDAE: OMALIINAE: ANTHOPHAGINI)

by

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Abstract

The rove beetle genus *Phlaeopterus* contained 15 species prior to this work, which are found in mountainous regions of northwestern North America, and in East Siberia for one species. These beetles can be found in perpetually cold, wet habitats, usually living in close association with permanent or long-lasting alpine snowfields. Very little is known of the life history of *Phlaeopterus*, but they have been observed on the surface of snowfields mating as well as feeding on windblown arthropods that have become stranded on snowfield's surface. In this thesis, I present a taxonomic revision of the genus *Phlaeopterus* as well as a phylogeny using Bayesian and maximum likelihood methods with 46 morphological characters and the mitochondrial gene COI. I found discordance between the morphological and molecular phylogenies, as well as between maximum likelihood and Bayesian methods. *Phlaeopterus castaneus* and *Phlaeopterus loganensis*, species with distinct morphology but identical COI sequence data, appear to have undergone recent hybridization in the Rocky Mountains where their ranges overlap. I found strong support for the synonymy of the monotypic genus *Vellica* with *Phlaeopterus*. Published taxonomic hypotheses were mostly supported and *a priori* hypotheses received mixed support. Additionally, the genus *Phlaeopterus* is re-described, a dichotomous key of all species is provided, and eight new species are described. Two of these, *Phlaeopterus bakerensis* n. sp., and *Phlaeopterus olympicus* n. sp., are highly endemic snowfield-associated species, and have not been collected since the late 1970s and early 1980s respectively, lending concern to their conservation status.

Dedicated to Ronald J. Palac (1949–2017).

For fostering my lifelong fascination with the natural world, and for unending encouragement of my intellectual pursuits.

Nomenclatural Statement

Taxonomic changes, names, and descriptions of new species included in this thesis are not formally published according to the International Code of Zoological Nomenclature (ICZN; Article 8.2) and are therefore not available names. Please wait for formal publication of these taxonomic acts before recognizing them.

Table of Contents

List of Figures

Page

List of Tables

Page

List of Appendices

Page

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Author contributions: L. J. Mullen wrote both manuscripts, collected morphological and molecular data, performed all data analyses, and produced all photographic, some line drawing, and all distribution map figures. J. M. Campbell discovered the 8 species credited to him, developed morphological character systems, proposed most taxonomic changes, proposed *a priori* species-group hypotheses, and produced all SEM and most line drawing

figures. D. S. Sikes provided intellectual guidance, extensive reviews of the manuscripts, and procured specimens and other required materials.

Introduction

Beetles have fascinated scientists throughout the history of Western Civilization, and likely beyond. Charles Darwin and Alfred Russell Wallace were avid beetle collectors, and J.B.S Haldane once famously remarked that if he had learned anything about the Creator it was that it must have an inordinate fondness for stars and beetles (Hutchinson, 1959). This attention can largely be attributed to the astounding diversity of beetles, which account for approximately 1 out of every 4 named species on the planet (Hammond, 1992). More staggering yet, the vast majority of beetle species are likely still undescribed (Erwin, 1982). Staphylinidae Latreille, 1802, or the rove beetles, is not only the largest family of beetles, but the single largest family of living organisms with over 62,780 described species, with an estimated 100–150 taxonomists dedicated to describing staphylinid diversity (Newton, unpublished data).

The staphylinid subfamily Omaliinae MacLeay, 1825, is characterized by a pair of ocelli, or simple eyespots, on top of the head, although the ocelli are absent from scattered taxa in the subfamily (Newton and Thayer 1995). Omaliinae is moderately large among the 32 staphylinid subfamilies, containing approximately 1,500 species (Zanetti *et al.* 2016), and was divided into seven tribes by Newton and Thayer (1995). The phylogeny of Newton and Thayer (1995) analyzes the relationships among omaliine tribes, but many of these relationships could not be resolved with their morphological dataset. Furthermore, no omaliine genera have been analyzed with modern phylogenetic methods, although Thayer (1985) performed a morphology-based parsimony analysis of the Australian genus *Metacorneolabium* Steel, 1950 by hand. A particularly challenging omaliine tribe for both taxonomic and phylogenetic analyses is Anthophagini Thomson, 1859. Anthophagini is

likely not monophyletic, lacks synapomorphies for all included taxa, and has been described as a taxonomic dumping ground (Newton *et al*. 2000). Modern taxonomic work on Anthophagini has been limited. Palearctic species of the genus *Lesteva* Latreille, 1797 have recently been described at a high rate (e.g., Shavrin *et al*. 2007, Shavrin 2010, 2014, 2015), and a new genus described from a Jurassic fossil from China was tentatively placed in the tribe (Cai and Huang 2013), but only 7 of the 27 North American anthophagine genera have been taxonomically revised (Campbell 1978, 1982, 1983, and 1984).

Phlaeopterus Motschulsky, 1853 is the most speciose of the 27 North American genera of Anthophagini, and contained 15 species prior to this work. The genus was described by Motschulsky (1853), with additional species described by Fauvel (1878), Casey (1885, 1886, 1894), Hatch (1957), and Shavrin (2001). Diagnoses of the genus have been published by Hatch (1957), Moore & Legner (1979), Newton *et al.* (2000), and Shavrin & Mullen (2015). The genus is found throughout mountainous regions of northwestern North America at the edges or on the surface of high-altitude and long-lasting snowfields and meltwater-fed streams. Adult beetles have been observed foraging on the surface of snowfields for frozen invertebrates and mating on the surface of the snow. *Phlaeopterus* larvae have never been described.

My specific aims in this thesis are to taxonomically revise the genus *Phlaeopterus* and provide the first reconstruction of phylogenetic relationships among *Phlaeopterus* species. In Chapter 1, I re-describe the genus *Phlaeopterus*, describe or re-describe all *Phlaeopterus* species, provide a diagnostic key for their identification, and map their distributions. In Chapter 2, I estimate the phylogeny of the genus using Bayesian and maximum likelihood methods with morphological and molecular data. I use this phylogeny

to test generic and species-level hypotheses of published works as well as *a priori* species-group hypotheses.

Literature Cited

Cai, C.Y. and Huang, D.Y., 2013. Sinanthobium daohugouense, a tiny new omaliine rove beetle (Coleoptera: Staphylinidae) from the Middle Jurassic of China. *The Canadian Entomologist*, *145*(5), pp.496-500.

Campbell, J.M., 1978. A revision of the North American Omaliinae (Coleoptera: Staphylinidae) 1. The genera *Haida* Keen, *Pseudohaida* Hatch, and *Eudectoides* new genus. *Memoirs of the Entomological Society of Canada*, 110(106), 1–20.

Campbell, J.M., 1982. A revision of the North American Omaliinae (Coleoptera: Staphylinidae): 3. The genus *Acidota* Stephens. *The Canadian Entomologist*, 114(11), 1003–1029.

Campbell, J.M., 1983. A revision of the North American Omaliinae (Coleoptera: Staphylinidae): 4. The genus *Olophrum* Erichson. *The Canadian Entomologist,* 115(6), 577–622.

Campbell, J.M., 1984. A revision of the North American Omaliinae (Coleoptera: Staphylinidae): 5. The genera *Arpedium* Erichson and *Eucnecosum* Reitter. *The Canadian Entomologist,* 11(6), 487–527.

Casey, T.L., 1885. New genera and species of Californian Coleoptera. *Bulletin of the California Academy of Sciences*, 7, 281–606.

Casey, T.L., 1886. Descriptive notices of North American Coleoptera I. *Bull. Cal. Acad. Sci.,* 2(6), 157–264.

Casey, T.L., 1894. Coleopterological Notices VI. *Annals of the New York Academy of Sciences*, 8(1), 435–838.

Erwin, T.L., 1982. Tropical forests: their richness in Coleoptera and other arthropod species. *Coleopterists Bulletin*, *36*(1), 74–75.

Fauvel, A., 1878. Les Staphylinides de l'Amerique du Nord. *Notices Entomologiques* 7, 1–100.

Hammond, P., 1992. Species inventory. In *Global biodiversity* (pp. 17-39). Springer Netherlands.

Hatch, M.H., 1957. The beetles of the Pacific Northwest: Part II: Staphyliniformia. University of Washington Press: Seattle, WA, USA.

Hutchinson, G.E., 1959. Homage to Santa Rosalia or why are there so many kinds of animals?. *The American Naturalist*, *93*(870), pp.145-159.

Latreille, P.A., 1797 Précis des caractères génériques des insectes, disposés dans un ordre naturel. F. Bourdeaux, Brive, 201 pp.

Latreille, P. A., 1802. Histoire naturelle des fourmis, et recueil de mémoires et d'observations sur les abeilles, les araignées, les faucheurs, et autres insectes. Paris, 445 pp.

Macleay, W.S., Horsfield, T., 1825. Annulosa javanica, or, an attempt to illustrate the natural affinities and analogies of the insects collected in Java by Thomas Horsfield.

Motschulsky, V.I., 1853. Nouveautés. *Etudes Entomologiques*, 1: 77–80.

Moore, I., Legner, E.F. 1979 An illustrated guide to the genera of the Staphylinidae of America North of Mexico exclusive of the Aleocharinae (Coleoptera). Division of Agricultural Sciences, University of California Priced Publication, 4093, 332 pg.

Newton, A.F. and Thayer, M.K., 1995. Protopselaphinae new subfamily for Protopselaphus new genus from Malaysia, with a phylogenetic analysis and review of the Omaliine Group of Staphylinidae including Pselaphidae (Coleoptera). *Biology, phylogeny, and classification of Coleoptera: papers celebrating the 80th birthday of Roy A. Crowson. Muzeum i Instytut Zoologii PAN, Warszawa*, pp. 219-320.

Newton, A.F., Thayer, M.K., Ashe, J.S., Chandler, D.S., 2000. 22. Staphylinidae Latreille, 1802. *In: Arnett, R.H. & Thomas, M.C. (Ed.), American Beetles, Vol. 1. Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia*, pp. 272–418.

Shavrin, A.V., 2001. New and little-known species of Omaliinae from the Baikal-Transbaikal area (Coleoptera: Staphylinidae). *Zoosystematica Rossica*, 9(1), 189–193.

Shavrin, A.V., 2010. Three new species of the genus Lesteva Latreille, 1797 (Coleoptera: Staphylinidae: Omaliinae: Anthophagini) from Uzbekistan, Tadzhikistan and Afghanistan. *Baltic Journal of Coleopterology*, 10(2): 147–152.

Shavrin, A.V., 2014. Review of the genus *Lesteva* Latreille, 1797 (Coleoptera: Staphylinidae: Omaliinae: Anthophagini) of Iran and adjacent territories. *Zootaxa*, 3884(2): 122–140.

Shavrin, A.V., 2015. New data on Himalayan *Lesteva* Latreille, 1797 (Coleoptera: Staphylinidae: Omaliinae) with description of a new species from Nepal. *Zootaxa*, 3973(3): 528.

Shavrin, A.V., Mullen, L.J., 2015. *Phlaeopterus* Motschulsky, 1853 (Coleoptera: Staphylinidae: Omaliinae: Anthophagini)-a new genus for the Palaearctic: new combination. *Zootaxa*, 4028(1), 121–128.

Shavrin, A.V., Shilenkov, V.G. and Anistschenko, A.V., 2007. Two new species and additional records of *Lesteva* Latreille, 1797 from the mountains of South Siberia (Coleoptera: Staphylinidae: Omaliinae: Anthophagini). *Zootaxa*, 1427: 37–47.

Steel, W.O., 1950. Notes on the Omaliinae (3). A new tribe and three new genera from New Zealand. Entomologist's Monthly Magazine 86: 54-64.

Thayer, M.K., 1985. Revision, phylogeny and biogeography of the austral genus Metacorneolabium Steel (Coleoptera: Staphylinidae: Omaliinae)[pp. 113–179]. *Taxonomy, phylogeny and zoogeography of beetles and ants (GE Ball, editor). Dr. W. Junk, Dordrecht*.

Thomson, C.G. 1859. Skandinaviens Coleoptera, synoptiskt bearbetade, vol. 1. Berlingska Boktryckeriet, Lund, 290 pp.

Zanetti, A., Perreau, M. and Solodovnikov, A., 2016. Two new fossil species of Omaliinae from Baltic amber (Coleoptera: Staphylinidae) and their significance for understanding the Eocene-Oligocene climate. *Arthr. Syst. Phylog*, *74*, pp.53-64.

Chapter 1 Taxonomic Revision of the Rove Beetle Genus *Phlaeopterus* Motschulsky, 1853 (Coleoptera: Staphylinidae: Omaliinae: Anthophagini)[1]

1.1 Abstract

The genus *Phlaeopterus* Motschulsky, 1853 is revised and a key to the 18 valid species is provided. Eight new species are described: *Phlaeopterus obsoletus* **new species**, *Phlaeopterus kavanaughi* **new species**, *Phlaeopterus bakerensis* **new species**, *Phlaeopterus smetanai* **new species**, *Phlaeopterus occidentalis* **new species**, *Phlaeopterus olympicus* **new species**, *Phlaeopterus hatchi* **new species**, and *Phlaeopterus elongatus* **new species**. Two species, *Phlaeopterus kootenayensis* Hatch, 1957, and *Phlaeopterus stacesmithi* Hatch, 1957, are transferred to the genus *Unamis* Casey, 1893, **new combination.** The monotypic genus *Vellica* Casey, 1885 is synonymized under *Phlaeopterus* **new synonymy.** *Phlaeopterus rufitarsus* Casey, 1893 is synonymized under *Phlaeopterus filicornis* **new synonymy.** *Phlaeopterus cascadiensis* is demoted to a subspecies of *Phlaeopterus castaneus* Casey, 1893, **new synonymy and new status**. *Phlaeopterus brevipennis* Casey, 1893 and *Phlaeopterus longipalpus* Casey, 1885 are synonymized under *Phlaeopterus cavicollis* Fauvel, 1878, **new synonymy.** Given these beetles' association with shrinking alpine snowfields, conservation concern is warranted, and some highly endemic species described herein have not been documented in over 35 years.

[1] Mullen, L.J., Campbell, J.M., Sikes, D.S., In Prep. Taxonomic Revision of the Rove Beetle Genus *Phlaeopterus* Motschulsky, 1853 (Coleoptera: Staphylinidae: Omaliinae: Anthophagini).

1.2 Introduction

Phlaeopterus Motschulsky, 1853 is a genus of moderately sized (3–10 mm) brown to black beetles (Figs. 1.1–1.5), and contained 15 species prior to this taxonomic revision. Members of *Phlaeopterus* are found throughout mountainous regions of northwestern North America as well as one species, *Phlaeopterus czerskyi* (Shavrin, 2001) from East Siberia (Shavrin and Mullen 2015, Figs. 1.6–1.14). These beetles are primarily found at the edges and on the surface of high-altitude and long-lasting snowfields up to 3,830 m elevation (Papp 1978, Wipfler *et al*. 2014, Table 1.1), where they have been observed foraging on arthropod fallout including psyllids, chironomids, lygaeids, and carabids (Papp 1978). One species, *P. cavicollis,* has been observed mating on the surface of snowfields, and has also been observed flying (J.M. Campbell, pers. obs.). Fourteen of the 18 species recognized here usually have fully developed wings, two species usually have wings brachypterous, and two species are always brachypterous. At lower latitudes, *Phlaeopterus* can be found foraging on snowfields only at night, but in British Columbia and Alaska are more likely to also be found foraging during the day (J.M. Campbell, pers. obs.). They can also be found under rocks and in moss in perpetually cold, moist environments including snowfield meltwater-fed and otherwise cold streams, meltwater-fed and high-altitude lakes, the splash zones of waterfalls, and occasionally at lower elevations including coastal areas and at the edges of cold springs or fast streams that stay cold in lower elevations (J.M. Campbell, L.J. Mullen, pers. obs.). Aside from these observations, the life history of these beetles is unknown and the larvae have never been described.

Phlaeopterus belongs to the tribe Anthophagini Thomson, 1859 which contains approximately 40 genera in the Holarctic and Oriental regions with approximately 112 species in 27 genera known from North America (Newton *et al*. 2000, Moore 1966). *Phlaeopterus* is the most speciose of the North American genera, although *Lesteva* contains ca. 109 described species globally (Herman 2001, Shavrin 2014) and species are still being described at a high rate (e.g. Shavrin *et al*. 2007, Shavrin 2010, Shavrin 2014, Shavrin 2015). Prior to this revision, only five anthophagine genera had been taxonomically revised (Campbell 1978, 1979, 1982, 1983, and 1984). Anthophagini is likely not monophyletic; it has been referred to as a taxonomic dumping ground and lacks synapomorphies for all included genera (Newton *et al*. 2000). The majority of the tribe can be diagnosed by the following combination of characters: metatarsi with tarsomeres 1–4 together or even separately longer than tarsomere 5, tarsomeres 1–4 subequal in width to tarsomere 5, tarsomeres 1–4 usually decreasing in length; antennae filiform, antennomeres 8–10 elongate to quadrate, maxillary palpomere segment 4 well developed (not highly reduced or sunken into apex of segment 3 as in Coryphiini Jacobson, 1908), segment 4 equal to or longer than 3, segment 4 usually approximately as wide as long, segment 4 wider than length of segment 3 (Newton *et al*. 2000, Moore 1966, Moore and Legner 1979). Adults often have relatively long legs and long elytra that cover most of the abdomen (Newton *et al*. 2000).

1.3 Taxonomic history of *Phlaeopterus* Motschulsky, 1853

1853 Motschulsky: 78 [original description]

1866 LeConte: 375 [misspelling] as *Phloeopterus*

1885 Casey: 318 [misspelling] as *Phloeopterus*

1886 Casey: 234 [misspelling] as *Phloeopterus*

1933 Scheerpeltz: 1065 [misspelling] as *Phloeopterus*

1952 Blackwelder: 303

1957 Hatch: 49

1961 Arnett: 240

1966 Moore: 49

1974 Moore and Legner: 551

1979 Moore and Legner: 208

2000 Newton *et al.*: 340

2015 Shavrin and Mullen: 1

= *Lesteva* Latreille, 1797 *sensu* Mäklin, 1853

1853 Mäklin: 193

= *Tilea* Fauvel, 1878

1878 Fauvel: 246 [original description]

1883 LeConte *et al.*: 104

1893 Casey: 402

1910 Bernhauer and Schubert: 74

= *Vellica* Casey, 1885 **new synonym**

1885 Casey: 321 [original description]

1893 Casey: 398

1952 Blackwelder: 403

1957 Hatch: 61

1961 Arnett: 240

1966 Moore: 48

1974 Moore and Legner: 551

1979 Moore and Legner: 199

2000 Newton *et al*.: 341

The genus *Phlaeopterus* was erected by Victor Motschulsky in 1853 to contain a single species, *Phlaeopterus fusconiger*. Motschulsky's diagnosis of the genus was minimal and restricted to differentiating *Phlaeopterus* from similar beetles that occur at the type locality – Unalaska, an island in the Fox Islands group of the Alaskan Aleutian Islands. He defined the genus as having short elytra in comparison to *Lyrosoma* Mannerheim, 1853.

Subsequently, but during that same year, Mäklin (1853) moved *Phlaeopterus fusconiger* to the genus *Lesteva* Latreille, 1797, (becoming *Lesteva fusconigra*) thereby making *Phlaeopterus* a synonym under *Lesteva*.

Apparently unaware of, or ignoring, Mäklin's (1853) work, which synonymized *Phlaeopterus* under *Lesteva,* T.L. Casey described two additional *Phlaeopterus* species: *Phloeopterus* [sic] *longipalpus* Casey (1885), and *Phloeopterus* [sic] *filicornis* Casey (1886). Then Casey (1893) transferred *P. fusconiger*, the type species of *Phlaeopterus*, to *Tilea* Fauvel, 1878, which synonymized the genus *Phlaeopterus* under *Tilea*. Casey (1893) noted that his "*Phloeopterus*" was a misspelling of *Phlaeopterus* Motschulsky. Casey (1893) also described three additional species: *Tilea brevipennis*, *Tilea castanea*, and *Tilea rufitarsis*. The genus *Tilea* had previously been monotypic, containing only *Tilea cavicollis* Fauvel, 1878, and thus contained a total of seven species after Casey's (1893) synonymy and

descriptions. However, Casey's (1893) synonymy of *Phlaeopterus* under *Tilea* violated the Principle of Priority (International Commission on Zoological Nomenclature 1999) because *Phlaeopterus* Motschulsky, 1853 is the older, and therefore senior name to *Tilea* Fauvel, 1878.

Scheerpeltz (1933) corrected the *Tilea-Phlaeopterus* synonymy to follow priority and placed *Tilea* as the junior synonym under *Phloeopterus* [sic].

Hatch (1957) included four *Phlaeopterus* species known from the Pacific Northwest in his key (excluding *P. fusconiger*, *P. filicornis*, and *P. castaneus*) and described seven additional species: *P. cascadiensis, P. frosti*, *P. houkae*, *P. kootenayensis*, *P. lagrandeuri, P. loganensis*, and *P. stacesmithi*. Hatch's (1957) contributions resulted in a total of fourteen *Phlaeopterus* species.

A revision of the genus *Phlaeopterus* was drafted, but never published, by J. M. Campbell in the 1980's (cited here as "Campbell (unpublished)"). This manuscript was to be the sixth installment in a series of revisions of the North American omaliine Staphylinidae (Campbell 1978, 1979, 1982, 1983, and 1984). Starting with the fourteen *Phlaeopterus* species recognized at the time, Campbell (unpublished) recognized a total of 17 *Phlaeopterus* species, 8 of which were new species. Furthermore, Campbell (unpublished) proposed the synonymy of the monotypic genus *Vellica* Casey, 1885 under *Phlaeopterus* and the transfer of two *Phlaeopterus* species to the genus *Unamis* Casey, 1983, the synonymy of one *Phlaeopterus* species under another, and the demotion of two others from species to subspecies. Although this work was never published, over 2,400 type specimens were designated and deposited in museum collections. The taxonomic acts

proposed in Campbell (unpublished) are recognized here, except where noted, and the 8 new *Phlaeopterus* species are described here.

Most recently, *Lesteva czerskyi* Shavrin, (2001) was re-described and transferred to *Phlaeopterus* by Shavrin and Mullen (2015), thus raising the number of published *Phlaeopterus* species to 15. *Phlaeopterus czerskyi* is known only from the Khamar-Daban Mountains of Eastern Siberia, and is the first species of the genus known outside of North America, thus confirming Casey's (1893) speculation that the genus likely occurs in Siberia.

The goals of this work are to describe or re-describe all species of *Phlaeopterus*, provide a key for their identification, and map their distributions.

1.4 Materials and Methods

We examined 2,635 specimens for this study representing all *Phlaeopterus* species (http://arctos.database.museum/saved/Phlaeopterus). These specimens are deposited at the 35 institutions listed in Appendix 1.1. Specimens generously donated by Alexey Shavrin, Link Olson, Jessica Rykken, Kip Will, and Jim LeBonte, and those collected by Derek Sikes and Logan Mullen are deposited in the University of Alaska Museum (UAM) Insect Collection.

1.4.1 Microscopy, Illustrations, and Photography

All specimens were examined with a Leica MZ16 stereomicroscope (Leica Microsystems, Wetzlar, Germany). High-resolution photographs were taken with a Stackshot z-stepper, a Canon 5D SLR camera with a 65mm macro lens and three Speedlight 580EX II flash units as part of the Passport Storm © system (Visionary Digital™ 2012) run

on Canon Utility and Adobe Lightroom 3.6 software. Zerene Stacker 1.04 software controlled the Stackshot z-stepper with images processed using the P-Max protocol. Montage photographs were adjusted for lighting and cropped in Adobe Photoshop CS6. Line drawings were based on photographs taken and assembled using the described methods, then traced in Adobe Illustrator CS6. All SEM images and some line drawings are adopted from Campbell (unpublished) and Shavrin and Mullen (2015). Permission for use of unpublished SEM images and line drawings is given by Agriculture and Agri-Food Canada and A.V. Shavrin, respectively (Appendix 1.2).

1.4.2 Databasing and Georeferencing

We selected specimens that together would be representative of each species' distribution by scanning the available material (over 11,000 specimens) for novel localities of each species. We attempted to database all type specimens, but did not database all paratype specimens (over 800 are designated for one species). We databased a subset of specimens of common species from as many unique localities as was feasible. Distribution maps were generated from these georeferenced Arctos records and visualized in SimpleMappr (Shorthouse, 2010). In an attempt to approximate absence data, we overlaid the collection localities of each species on all georeferenced *Phlaeopterus* localities in each distribution map. This provides an indication of where effort appropriate to the collection of *Phlaeopterus* was successfully applied and thus also indicates areas where no such effort has been applied, to the best of our knowledge. These areas lacking prior successful collections would be ideal to target to fill in range gaps.

1.4.3 Species Delimitation and Species Concept

Our species delimitation methods were primarily those of morphological diagnosibility, although the species hypotheses recognized here were tested in the morphological and molecular (mitochondrial COI) phylogeny of Chapter 2, and this phylogeny is discussed where relevant. It is our expectation that these species reflect separately evolving metapopulation lineages, as outlined by De Queiroz (2007).

1.4.4 Morphological Characters

We coded 46 morphological characters in Mesquite 3.04 (Maddison and Maddison 2016) then exported these using the plain language option (File: Export File: Descriptions) in MacClade 4.06 (Maddison and Maddison 2005) and edited for clarity of language. For additional details about this morphological data matrix, which draws most characters from Campbell (unpublished), see Chapter 2. Descriptions were then augmented with additional characters from Moore and Legner (1979), and Campbell (unpublished), the latter being characters not included in the data matrix of Chapter 2 because they are not informative for the phylogeny of *Phlaeopterus* but are useful in diagnosing species. Based on the specimens we have examined, the most useful characters for diagnosing *Phlaeopterus* species seem to be the shape of the pronotum (especially the degree of explanation or deflection of the lateral margins, Figs. 1.15–1.17), the presence or absence of a glabrous region at the apex of the tibiae (Fig. 1.18), the carina of the mesosternum (Figs. 1.19–1.20), and the aedeagus (Figs. 1.21–1.26).

1.4.5 Genus and Species Descriptions

The genus description contains only characters informative for differentiating genera and higher taxonomic levels, and the species descriptions contain only characters informative for differentiating *Phlaeopterus* species. We have attempted to provide a comprehensive list of the usage of each name in the literature with year of publication, author, and page number. The publication with the original description of each name, and cases of name use in a different combination than that recognized here are noted. Aedeagal characters are described as viewed ventrally for characters of the parameres and median lobe, and dorsally for characters of the internal sack, with both views illustrated for all species but *P. czerskyi*, which instead has dorsal and lateral views illustrated. Observations of aedeagal characters were made from entire genitalia dissections, mounted on slides and suspended in glycerin, as well as from illustrations of J.M. Campbell (unpublished) and Shavrin and Mullen (2015), both of which are included here with permission (Appendix 1.2). In descriptions of specimen label data, different labels on the same type specimens are separated by "/", and is verbatim except for text in square brackets, which we have added for clarity. Remarks on the habitat of each species are based on field observations made by J.M. Campbell except where otherwise noted. Elevation ranges for each species are taken from the field observations of J.M. Campbell and subsequently modified with the elevation range of specimens georeferenced in this study. The elevation range of georeferenced specimens was derived from Google Earth for specimens without elevation label data. Specimens with vague locality data (e.g. "Denali National Park") were not considered in estimations of elevation range of each species.

1.5 Results

1.5.1 Diagnosis of the Genus Phlaeopterus

The genus *Phlaeopterus* can be distinguished from all other genera of the tribe Anthophagini by the following characters: 1) Head, pronotum, and elytra not especially finely, densely punctate (as in *Unamis* Casey, 1893, Figs. 1.27B–C, 1.15C–D); 2) Antennae with all segments with nearly equal density of pubescence; 3) Mandibles with inner margin with irregular row of setae and a single tooth; molar area with L-shaped row of setae (Figs. 1.28F, 1.29A–1.29C, 1.30C) or with separate oblique row of setae basally (Fig. 1.28E); 4) Labrum transverse (Figs. 1.31E–1.31H, 1.30B); 5) Maxillary palpi elongate, filiform, apical (fourth) segment subequal in width to penultimate (third) segment (Figs. 1.32C–1.32D, 1.30D); 6) Epipharynx with basal area smooth, lacking oblique ciliate ridges (Figs. 1.33E–1.33H); 7) Nuchal area surfaced with punctation and microsculpture which is undifferentiated from that of the vertex (Figs. 1.34, 1.35A–1.35B); 8) Nuchal constriction vague or lacking (Figs. 1.34, 1.35A–1.35B); 9) Mesosternum with anterior portion expanded into a medial projecting tooth and usually also with medial longitudinal carina (Figs. 1.19E–1.19F, 20); 10) Elytra 1.7–3.2 times longer than pronotum at midline; 11) Metatarsi with segments 1–4 together 2.2–3.8 times longer than segment 5; and 12) Aedeagus with internal sac elongate, sac like, partially or completely covered with microspinules (Figs. 1.21–1.26).

We confirmed the 18 species described or re-described herein fit this diagnosis. However, we did not examine the epipharynx of *P. czerskyi*. Two species, *Unamis kootenayensis* (Hatch, 1957), **new combination** and *Unamis stacismithi* (Hatch, 1957), **new**

combination do not fit the diagnosis of *Phlaeopterus* given above, and so are transferred to the genus *Unamis* where they belong based on the diagnostic characters of that genus: 1) nuchal constriction distinct (Figs. 1.27A–1.27B) and with microsculpture that is lacking on the vertex (Fig. 1.27C); 2) labrum short (Figs. 1.31C–1.31D); 3) epipharynx with apical portion elongate and smooth (Figs. 1.33C–1.33D); and 4) Pronotum and elytra with fine dense punctation (Newton *et al.* 2000, Moore, 1966, Moore and Legner, 1972).

1.5.2 Redescription of the Genus *Phlaeopterus*

Habitus. (Figs. 1.1–1.5) 2.7–10.1 mm long; broadly oval, often strongly dorso-ventrally flattened, rarely more elongate and convex; dorsal surface smooth, shining, pubescent and punctate; color reddish-brown to yellowish brown to black, head and abdomen usually darkest, pronotum and elytra often lighter, head, mouthparts, palpi, and legs often lightest.

Head. Head subquadrate to slightly transverse (Figs. 1.34, 1.35A–1.35D); width across eyes slightly narrower than the length of the head to broader than the length of the head. Eyes protruding beyond lateral margins of head; dorsal half glabrous, ventral half moderately pubescent or nearly to entirely glabrous (Fig. 1.36). Ocelli present (most species, Figs. 1.35A–1.35D) or absent (two species, *P. obsoletus* and *P. longipennis*, Fig. 1.34C–1.34D). Antennae elongate, filiform; segments 2–11 with nearly equal densities of pubescence; segments 5–10 greater than or equal to 1.4 times as long as wide; segments 4–11 each with many sensory pits either with groups of pore-like openings (1.37E) or papilliform projections (Figs. 1.37D, 1.37F), each pit less than 5 μm in diameter. Interantennal groove (dorsal transverse impression between antennal insertions) vague

and shallow or absent (Figs. 1.34, 1.35A–1.35B). Anteocellar foveae (dorsal impressions anterior of ocelli, roughly between eyes) shallowly (Fig. 1.34) to deeply (Figs. 1.35B–1.35C) impressed. Nuchal area dorsally surfaced with punctation and microsculpture that is undifferentiated from the punctation and microsculpture of the vertex (Figs. 1.34, 1.35A–1.35B). Nuchal constriction vague (most species, Figs. 1.34A, 1.34C, 1.35A–1.35B) or lacking (one species, *Phlaeopterus houkae*, Fig. 1.34B). Temples short, clearly differentiated to undifferentiated from nuchal area (Figs. 1.34, 1.35A–1.35B). Maxillary palpi long, filiform; penultimate (third) segment elongate, longer than wide, apical segment 1.4–3.4 times as long as penultimate (third, Figs. 1.32C–1.32D). Labial palpi (Fig. 1.32F) with third segment 1.1–1.8 times longer than second segment. Mandibles curved inwards, nested with left mandible held posterior and dorsad of right mandible, and pointed apically; inner margin with irregular row of setae and a single tooth (Figs. 1.28E–1.28F, 1.29A–1.29B); molar area with L-shaped row of setae (Figs. 1.28F, 1.29A–1.29C, 1.30C) or with separate oblique row of setae basally (Fig. 1.28E). Labrum transverse, widest near midline and narrowing toward apex and base, < 0.3 times as long as wide, with sensory pores along anterior margin or sensory pores along entire surface (Figs. 1.31E–1.31H). Epipharynx with basal area smooth, lacking oblique ciliate ridges, but with apically directed central patch of cilia and/or spines extending mediolaterally (Figs. 1.33E–1.33H). Maxilla with lacinia and galea moderately elongate and narrow; inner side of lacinia with dense row of long setae extending from base to apex (Figs. 38E–38F, 39). Hypopharynx with setae and/or spines haphazardly distributed basally, not organized into distinct oblique rows (Figs. 1.40E–1.40F, 1.41A–1.41C). Gula > 0.2 times as wide as mentum; mentum trapezoidal, widest at base, narrowing apically (Fig. 1.41E–1.41F, 1.42C–1.42F). Gular

sutures separate, subequally divergent anterior and posterior of narrowest point to more strongly divergent anterior than posterior of the narrowest point (Fig. 1.41E–1.41F, 1.42C–1.42F).

Thorax. Pronotal shape variable (Figs. 1.15E–1.15H, 1.16, 1.17A–1.17E): widest at some point laterad the apex and narrowing towards base to nearly rectangular. Pronotum 1.3–1.9 times wider than head width, slightly less than 0.7 to slightly greater than 0.9 times as long as wide, widest point of pronotum subequal to slightly narrower than width of elytra at base; pronotal disk convex in cross section, flanked by margins strongly explanate to strongly deflexed; with pair of lateral foveae ranging from deeply impressed to moderately impressed; punctures separated by distance less than the diameter of a puncture to twice as great as the diameter of a puncture; lateral margins smooth or crenulate in one species (*P. czerskyi*); inflexed sides of pronotum with acutely angulate postcoxal lobe extending medially to or slightly beyond level of protrochantin. Prosternum moderately long; intercoxal process acutely triangular, separating only anterior portion of procoxae; not keeled medially. Protrochantin broadly exposed. Mesosternum (Figs. 1.19E–1.19F, 1.20) with longitudinal carina along midline complete or reduced on posterior half or vague or absent in two species (*P. olympicus* and *P. loganensis*); anterior portion of longitudinal carina expanded posteriorly into a projecting tooth. Antemesosternal plate reduced, vaguely differentiated from other plates/sclerites; without anterolateral ridge; with acutely triangular process extending posteriorly to near middle of mesocoxae. Metasternum reduced and narrowly separated from anterior margin of metacoxae; with antecoxal suture absent or narrowly separated from anterior margin of metacoxae; with anterior margin

narrowly rounded medially and externally, projecting slightly between mesocoxae, lacking process between metacoxae. Metatrochanter with tooth present or absent. Elytra slightly longer than wide in one species (*P. bakerensis*) or distinctly longer than wide; 1.7–3.2 times longer than pronotum at midline, not covering entire abdomen, with elytra terminating over tergite IV to VI; humeral angles of elytra (Fig. 1.29F) convex with epipleural carina not projecting or rectangular with epipleural carina projecting; epipluera broad, ending just before elytral apex; epipleural ridge well developed; apical margins of elytra convex, subtruncate, or prolonged at elytral suture. Wings fully developed or brachypterous.

Legs. Legs long, with apex of each femur extending well beyond sides of body. All coxae contiguous; Procoxa elongate, conical; mesocoxa elongate; metacoxa triangularly elongate. Pro-, meso-, and metatibia with spine-like setae becoming more dense from base to apex, with dense pubescence, apex of tibia lacking pubescence but with spine-like setae (= subglabrous in species descriptions, Fig. 1.18) or with uniform pubescence to apex. Tarsi 5-segmented; protarsi short, segments 1–4 subequal in length, together 1.9-2.0 times longer than segment 5; metatarsi longer, segments 1–4 together 2.2–3.8 times longer than segment 5, first metatarsomere slightly shorter or longer than apical metatarsomere; second metatarsomere shorter than basal (first) metatarsomere. Metatibia 1.5–2.2 times longer than metatarsus.

Abdomen. Abdomen with tergite VIII visible in both sexes; pair of wing-folding spicules on tergites IV and V or on tergites IV, V, and VI or absent from all tergites in one species (*P. czerskyi*); shape of wing-folding patches on tergite V broadly oval and narrowly separate or

combined into a single transverse band; Sternites II and III each with small, median basal tooth projecting between metacoxae.

Aedeagus. (Figs. 1.21–1.26). Median lobe of aedeagus broadly triangular or narrowed with sides subparallel or elongate with apex broadly rounded; not carinate or with apical carina. Paramere length subequal to median lobe to extending beyond apex of median lobe. Internal sac long, sac-like, partially or completely covered with microspinules or patterns of sclerites.

Sexual dimorphism. Females tend to be slightly longer and wider than males, and often have longer elytra. Males have protibiae with tarsomeres broader and with longer and thicker ventral setae than females. Sexual variation in the length of the glabrous apical region of metatibia as a ratio to metatibia length is given in species descriptions where relevant. Females of *P. filicornis* and *P. elongatus* have the apex of the elytra prolonged at the suture (Fig. 1.29F), whereas males of these species have the apex of the elytra broadly convex. No other species of the genus are sexually dimorphic in shape of apex of the elytra although *P. loganensis* has the apex of the elytra prolonged at the suture in both sexes (Fig. 1.29E). Tergite VIII is the last segment visible in females (tergite VIII is female pygidium) whereas males have tergites IX and X visible (tergite X is male pygidium). Viewed dorsally, the female pygidium is broadly rounded while the male pygidium is triangular. In museum specimens, elongate and slender styli are often visible protruding from the female pygidium, and the internal sac of the aedeagus of males is sometimes exerted.

1.5.3 Dichotomous Key to Adults of Species of the Genus *Phlaeopterus* Motschulsky, 1853 of the World

1 Size less than 4.7 mm. Ocelli present (Figs. 1.35A–1.35B) or absent (Fig. 1.34C). Dorsal half of eye glabrous or pubescent but ventral half of eye usually with more than 10 setae (Figs. 1.36A–1.36C). Anteocellar foveae small, shallowly impressed (Figs. 1.34A–1.34B). 2

- Size greater than 4.8 mm. Ocelli present (Fig. 1.35A–1.35B). Entire eye glabrous or nearly glabrous with less than 10 setae near ventral or posterior margin (Figs. 1.36D–1.36F). Anteocellar foveae large, deeply impressed (Figs. 1.35A–1.35B). 6

2(1) Ocelli absent (Fig. 1.34C). 3

- Ocelli present (Figs. 1.35A–1.35B). 4

3(2) Head and pronotum moderately coarsely punctate (Fig. 1.4C). Median lobe of aedeagus broadly triangular (Fig. 1.21D). Distribution: Mt. Hood, Oregon north to southern British Columbia and southwestern Alberta. *P. obsoletus* n. sp.

- Head and pronotum finely punctate (Fig. 1.4B). Median lobe of aedeagus narrowly triangular (Fig. 1.21C). Distribution: Crater Lake, Oregon south to northern California. ..... *P. longipennis* (Casey)

4(2) Lateral margins of pronotum crenulate (Fig. 1.1D). Metatrochanter without tooth on apical margin. Elytra less than 1.9 times length of pronotum. Wing-folding spicules absent from all tergites. Distribution: Khamar-Daban Mountains, East Siberia. ..... *P. czerskyi* (Shavrin)

- Lateral margins of pronotum not crenulate (Figs. 1.15E–1.15F). Metatrochanter with or without tooth on apical margin. Elytra greater than 1.9 times length of pronotum. Wing-folding spicules present on tergites IV and V. Found in North America, not Siberia. 5

5(4) Metatrochanter with large tooth on apical margin (Fig. 1.40D). Elytra usually with distinctive yellow to reddish-yellow area as small spot on humeri to nearly covering elytral disc (Fig. 1.3D). Pronotum coarsely, sparsely punctate (Fig. 1.15E). Distribution: southeast Alaska, west central British Columbia south to northern California. ..... *P. lagrandeuri* Hatch

- Metatrochanter without tooth on apical margin. Elytra sometimes lighter than pronotum but without distinctive yellow to reddish-yellow area (Fig. 1.3C). Pronotum finely, densely punctate (Fig. 1.15F). Distribution: Alaska south to northern California, including Haida Gwaii and Vancouver Island. ..... *P. houkae* Hatch

6(1) Pronotum with lateral margins deflexed posterad the lateral foveae (Figs. 1.17C–1.17E). Apices of tibiae glabrous at least narrowly (Fig. 1.18). 7

- Pronotum with lateral margins explanate posterad the lateral foveae (Figs. 1.16, 1.17A–1.17B). Apices of tibiae glabrous (Fig. 1.18) or pubescent.

.....9

7(6) Pronotum narrow (Fig. 1.17E), ratio of length:width greater than 0.85. Tergite VI with pair of wing-folding spicules (Fig. 1.17H). Length 4.8-6.4 mm. Distribution: the Alaska Range, southern British Columbia, southwestern Alberta, and Wyoming.

.....*P. elongatus* n.sp.

- Pronotum wide (Fig. 1.17C–1.17D), ratio of length:width less than 0.85. Tergite VI lacking pair of wing-folding spicules. Length 5.5–7.7 mm.

.....8

8(7) Pronotum with distinct pair of foveae (Fig. 1.17C). Female (see genus description 'sexual dimorphism' to sex specimens) with apices of elytra triangular (Fig. 1.28F), longest just laterad of elytral suture and slightly diverging near apex of elytral suture, male with apex of elytra convex. Aedeagus with apex of median lobe long and narrow, internal sac evenly covered in small microspinules (Fig. 1.25C). Distribution: Sierra Nevada and Cascade Range of California.

.....*P. filicornis* Casey

- Pronotum lacking, or with only vague, pair of lateral foveae. Both sexes with apices of elytra convex (Fig. 1.3A). Aedeagus with median lobe shorter and broader, internal sac with patches of distinctly larger microspinules near apex (Fig. 1.25B). Distribution: southeastern Alaska, British Columbia south to northern California.

.....*P. hatchi* n.sp.

9(6) Pronotum with lateral margins broadly and subequally explanate anterad and posterad the lateral fovea (Fig. 1.16C–1.16D). 10

- Pronotum with lateral margins less broadly explanate anterad than posterad the lateral foveae, or explanate posterad but not explanate anterad the lateral foveae (Figs. 1.16A–1.16B, 1.16E–1.16H, 1.17A–1.17E). 11

10(9) Elytra with humeral angles projecting, carinate anteriorly (Fig. 1.29D). Pronotum broad, width across base nearly as wide as elytra across humeral angle (Fig. 1.16D, 1.1A). Size very large, 8.2–10.1 mm in length. Distribution: known only from Mt. Baker area of Washington. ..... *P. bakerensis* n.sp.

- Elytra with humeral angles broadly rounded, not carinate anteriorly. Pronotum narrower, width across base less than width of elytra across humeral angle (Fig. 1.16C, 1.1C). Size smaller, 6.3–9.2 mm in length. Distribution: widely distributed in western North America, Alaska south to California and east to Colorado. ..... *P. cavicollis* (Fauvel)

11(9) Tibiae, with apical portion nearly glabrous, contrasting with densely pubescent remainder of tibiae (Fig. 1.18). 12

- Tibiae densely and uniformly pubescent. 18

12(11) Elytra with apices broadly triangular, elongated at suture (Fig. 1.29E). Aedeagus with median lobe elongate, sides subparallel and slightly constricted at middle (Fig. 1.24C). Distribution: southeastern British Columbia, southwestern Alberta, Idaho, and Montana. ..... *P. loganensis* Hatch

- Elytra with apices convex to nearly truncate, longest at some point laterad the apex of the elytral suture. Aedeagus variable. 13

13(12) Mesosternum without median carina but with large posteriorly projecting posteromedial tooth (Fig. 1.20C). Aedeagus with apex of median lobe narrowly triangular, parameres straight (Fig. 1.24B). Distribution: Olympic Peninsula and Okanagan County, Washington. ..... *P. olympicus* n. sp.

- Mesosternum with median carina at least on anterior half and with posteriormedial tooth (Figs. 1.20D–1.20E). Aedeagus with median lobe broadly triangular, parameres curved medially (Figs. 1.24D, 1.25). 14

14(13) Black (Fig. 1.5B). Mesotibia with apical glabrous portion shorter than basal segment of mesotarsus. Pronotum with lateral margins narrowly explanate anterad the lateral foveae (Fig. 1.16E). Aedeagus with internal sac lacking a transverse fold (Fig. 1.23B–1.23C). Distribution: widely distributed in the Western United States from Washington south to California and Arizona and west to Colorado.

..... *P. smetanai* n.sp. (in part)

- Dark brown to reddish brown to yellowish brown (Figs. 1.2C, 1.2D, 1.4D). Mesotibia with apical glabrous portion longer than basal segment of mesotarsus.

Pronotum with lateral margins narrowly explanate (Fig. 1.16F) or not explanate (Figs. 1.17A–1.17B) anterad the lateral foveae, but if narrowly explanate then aedeagus with interal sac with a transverse fold. 15

15(14) Pronotum with lateral margins narrowly explanate nearly to apical margin (Figs. 1.16F, 1.4D). Aedeagus with internal sac with subapical transverse fold (Fig. 1.24A). Distribution: Alaska south to northern California and Sierra Nevada.

.....*P. occidentalis* n.sp.

- Pronotum with lateral margins explanate only to lateral foveae or slightly anterad the lateral foveae (Figs. 1.17A–1.17B). Aedeagus with internal sac rectangular, lacking a subapical transverse fold (Figs. 1.24D, 1.25A).

..... 16

16(15) Mesotibia with length of glabrous apical portion less than or equal to length of basal three mesotarsal segments combined (Fig. 1.18B). Aedeagus with internal sac short, lightly sclerotized (Fig. 1.24D). Distribution: Aleutian Islands south to Olympic Mountains of Washington. ..... *P. fusconiger* (Motschulsky)

- Mesotibia with length of glabrous apical portion subequal to length of basal four mesotarsal segments combined (Fig. 1.18A). Aedeagus with internal sac longer, more heavily sclerotized (Fig. 1.25A). Distribution: Alaska south to Oregon.

..... *P. frosti* Hatch

17(11) Black (Fig. 1.5B). Aedeagus with apex of median lobe broadly rounded, not carinate medially (Figs. 1.23B–1.23C). Distribution: widely distributed in western United States from Washington south to California and Arizona and west to Colorado.

..... *P. smetanai* n.sp. (in part)

- Dark brown to reddish brown to yellowish brown (Figs. 1.1B, 1.3C). Elytra often paler than pronotum. Aedeagus with apex of median lobe narrowly triangular to acuminate, carinate medially (Fig. 1.21E–1.21F, 1.22A).

.....18

18(17) Elytra reddish to yellowish brown, lighter color than pronotum (Fig. 1.3C). Aedeagus with apex of median lobe narrowly triangular (Fig. 1.21E). Pronotum with lateral margins gradually diverging from base to basal third (Fig. 1.16A). Distribution: Cascade Range of Oregon south to Northern California.

.....*P. kavanaughi* n.sp.

- Elytra and pronotum reddish brown, not noticeably different in color (Fig. 1.1B). Aedeagus with sides of median lobe abruptly narrowed just before apex (Fig. 1.21F, 1.22A). Pronotum with lateral margins slightly converging or subparallel at base then convexly diverging to basal half (Fig. 1.16B). Distribution: Alaska south to Cascade Range of Oregon and east through the Rocky Mountains.

.....*P. castaneus* (Casey)(two subspecies).....19

19(18) Pronotum with lateral margins usually narrowly explanate anterad the lateral foveae. Aedeagus with internal sac elongate, approximately 2/3^{rds} as long as aedeagus (Fig. 1.22A). Elytra usually uniformly dark reddish brown. Distribution: Alberta south to Colorado and west to eastern Oregon, eastern Washington, and Garibaldi Provincial Park, British Columbia.

..... *P. castaneus castaneus* (Casey)

- Pronotum with lateral margins usually not explanate anteriorly. Aedeagus with internal sac shorter, less than ½ as long as aedeagus (Fig. 1.21F). Elytra with sutural area lighter reddish brown than remainder of elytral surface. Distribution: Aleutian Islands and southeastern Alaska, Garibaldi Provincial Park, British Columbia south through the Cascade Range to Three Sisters, Oregon.

..... *P. castaneus cascadiensis* (Hatch)

1.5.4 Species Descriptions

1.5.4.1 *Phlaeopterus bakerensis* Campbell n. sp.

Figs. 1.1A, 1.6A, 1.16D, 1.23A, 1.29B, 1.29D, 32D, 36E

Type locality: Mt. Baker, Washington, USA

Habitus. (Fig. 1.1A) 8.2–10.1 mm in length. Dark brown to reddish brown; antennae and palpi reddish-brown; elytral epiplurae sometimes lighter.

Head. Head broad, ratio of width across eyes to length of head about 5:4. Interantennal groove broadly and deeply impressed. Anteocellar foveae large, deeply impressed. Eye pubescence absent (Fig. 1.36E). Antennae with segments 5–10 at least 2 times longer than wide; segments 4–11 each with many sensory pits with papilliform projections. Ocelli present. Nuchal constriction vague. Maxillary palpi (Fig. 1.32D). Mandibles with molar area with L-shaped row of setae (Fig. 1.29B). Labrum with sensory pores along entire surface. Labial palpi with third segment 1.6–1.8 times longer than segment 2.

Thorax. Pronotum wide (Fig. 1.16D), length to width ratio = 0.61–0.65; ratio of width of pronotum to width of head = 1.72–1.79; maximum width subequal to elytra width at humeral angle; punctures on dorsal surface separated by average distance slightly greater than diameter of one puncture; lateral margins broadly explanate anterad and posterad the lateral foveae; lateral foveae deeply impressed. Elytra with humeral angles projecting (Fig. 1.29D); epipleural carina projecting; 2.0–2.3 times longer than pronotum; apical margins broadly convex. Wings nearly always fully developed, rarely brachypterous. Mesosternum with projecting tooth; longitudinal carina along midline of mesosternum complete.

Legs. Pro-, meso-, and metatibia with dense pubescence to apex or with small subglabrous region at apex, subglabrous apex of mesotibia less than or equal to length of basal mesotarsomere. Metatrochanter without tooth on apical margin.

Abdomen. Wing-folding spicules on tergites IV and V broad, transverse, narrowly separated; tergite VI lacking wing-folding spicules.

Aedeagus. (Fig. 1.23A) 1.60–1.73 mm long. Median lobe abruptly narrowed just before apex. Parameres subparallel near base, nearly evenly convex for remainder; ending past apex of median lobe. Internal sac oblong; lightly sclerotized, microspinules more dense on basal half.

Type specimens. Holotype male (UAMObs:Ento:235822), and allotype female (UAMObs:Ento:235823), each with labels as follows: WASH., Mt. Baker, Heather Meadows, 23.VII.1979, 4000', J.M. & B.A. Campbell/ HOLOTYPE ♂ (or ALLOTYPE ♀) *Phlaeopterus bakerensis* desig. J.M. Campbell CNC No. 18468. Both specimens are in the CNC, Ottawa. Paratypes: 184, deposited in AMNH, RBCM, CAS, CSCA, CNC, FMNH, MCZ, ROM, USNM, UCRC.

Distribution. (Fig. 1.6A) *Phlaeopterus bakerensis* is known only from Mt. Baker and Mount Baker-Snoqualmie National Forest, Washington at elevations of 1220–1500 m. Adults have been collected at night on the surface of snowfields during the month of August, where they have been observed feeding on arthropods (mostly Diptera) or during the day under rocks at edges of snowfields. We found one additional specimen of this species in the J. Jarrige collection, Schmitt box 359, in the MNHN, Paris, with nearly illegible label data that we tentatively interpret as follows: Austin Pass N.W. Cass. OR. [illegible, possibly niv co.] 1600 m 27.VII.62 G.D./Phlaeopterus m.h. [possibly a reference to Melville Hatch]/Phlaeopterus

bakerensis n. sp. det. L.Mullen 2015. This specimen suggests that *P. bakerensis* may also occur in Oregon, but should be regarded with suspicion unless confirmed by additional collection records. This specimen was not included in the range map of *P. bakerensis* due to our uncertain interpretation of the locality data.

Remarks. *Phlaeopterus bakerensis* is, to our knowledge, the largest species in the entire subfamily Omaliinae. It can be easily distinguished from all other *Phlaeopterus* species by its large size, broad pronotum, and projecting humeral angles of the elytra. This species has not been collected since 1979 (http://arctos.database.museum/saved/Phlaeopterus%5Fbakerensis), and so would be an ideal candidate for recollection efforts.

Etymology. This species was named for the type locality of Mt. Baker, Washington.

1.5.4.2 *Phlaeopterus castaneus* (Casey)

Figs. 1.1B, 1.6B, 1.16B, 1.21F, 1.22A

Type locality: Colorado

1893 Casey: 403 [original description] original combination: *Tilea castanea*

1975 Moore and Legner: 208

1991 Davies: 5

= *cascadiensis* Hatch, 1957 **new status as subspecies and synonymy**

1957 Hatch: 59 [original description]

1991 Campbell and Davies: 5

Habitus. (Fig. 1.1B) 5.6–7.7 mm in length. Dark brown to reddish brown; lateral margins of pronotum often lighter; head, elytra, palpi, and antennae sometimes lighter.

Head. Head moderately broad, ratio of width across eyes to length of head = 1.0–1.3. Interantennal groove broadly and deeply impressed. Anteocellar foveae large, deeply impressed. Eye pubescence absent, or with less than 10 scattered setae near ventral margin. Antennae with segments 5–10 at least 2 times longer than wide; segments 4–11 each with many sensory pits with papilliform projections. Ocelli present. Nuchal constriction vague. Mandibles with molar area with L-shaped row of setae. Labrum with sensory pores along entire surface. Labial palpi with third segment 1.6–1.8 times longer than segment 2.

Thorax. Pronotum (Fig. 1.16B) broad, length to width ratio = 0.63–0.73; ratio of width of pronotum to width of head 1.5–1.61; maximum width subequal to elytra width at humeral angle; punctures on dorsal surface separated by average distance equal to twice diameter of single puncture; lateral margins explanate posterad the lateral foveae, narrowly explanate to not explanate anterad the lateral foveae; lateral foveae deeply impressed.

Elytra with humeral angles convex; epipleural carina not projecting; 2.2–2.5 times longer than pronotum; apical margins broadly convex. Wings nearly always fully developed, rarely brachypterous. Mesosternum with projecting tooth; longitudinal carina along midline of mesosternum complete but not strongly carinate.

Legs. Pro-, meso-, and metatibia with dense pubescence from base to apex. Metatrochanter without tooth on apical margin.

Abdomen. Wing-folding spicules on tergites IV and V broad, transverse, narrowly separated; tergite VI lacking wing-folding patches.

Aedeagus. Aedeagus of *P. castaneus cascadiensis* (Fig. 1.21F), 1.20–1.36 mm long, *P. castaneus castaneus* (Fig. 1.22A), 1.32–1.48 mm long. Median lobe narrowed abruptly just before apex, with longitudinal carina at apex. Parameres narrow. Internal sac variable; 2/3rds to ½ length of median lobe; covered in microspinules; with or without subapical transverse fold.

Type specimens. Lectotype male (UAMObs:Ento:235783), with label data as follows: Col./♂/CASEY bequest 1925/TYPE USNM 48100/[Tilea] Castanea [sic]/LECTOTYPE ♂ Phlaeopterus castanea (Casey) des. 1984, J.M. Campbell. Paralectotype male with label data as follows: CASEY bequest 1925/castanea PARATYPE USNM 48110. Holotype male (UAMObs:Ento:235219), and allotype female (UAMObs:Ento:235777), with label data as follows: Mt. Rainier, WASH., Tipsoo Lake, Aug. 2, 1938, M.H. Hatch/TYPE ♂ (or ALLOTYPE

♀) Phlaeopterus cascadiensis 1951 – M.H. Hatch. All four specimens are in the USNM, Washington, DC.

Distribution. (Fig. 1.6B) P*hlaeopterus castaneus* is known from the Aleutian Islands and Southeast Alaska, the Rocky Mountains and Coast Range from British Columbia south to Utah and Colorado, and the Cascade Range of British Columbia south to Oregon. This species has been collected at elevations of 500–2500 m at the edges of cold, fast streams and sometimes at the edges of snowfields and lakes fed by melting snow. We have confirmed the surprising occurrence of this species on Unalaska Island from a single specimen (UAMObs:Ento:233345).

Remarks. *Phlaeopterus castaneus* can be distinguished from all other *Phlaeopterus* species by the shape of the pronotum, tibiae evenly pubescent to apex, mesosternum weakly but completely carinate, and by the shape of the aedeagus. We have chosen to demote *Phlaeopterus cascadiensis* to a subspecies of *Phlaeopterus castaneus* **new synonymy and status** primarily because of the abundance of intermediate forms at the zone of overlap of the two. The two subspecies can be distinguished throughout most of their range by the length and microspinules of the internal sac of the aedeagus, the explanate lateral margins of the pronotum, and to some extent the coloration of the elytra. However, in Garibaldi and Manning Provincial Parks intermediate states of microspinules of the internal sac and the explanate lateral margins of the pronotum can be found. Phylogenetic analysis of Chapter 2 recovered the two subspecies as two distinct clades based on mitochondrial COI sequence data, but also found evidence of hybridization between *P. castaneus castaneus* and *P.*

loganensis, which co-occur in the Rocky Mountains. The two subspecies are diagnosable throughout their range except in the zone of overlap in Garibaldi and Manning Provincial Parks, British Columbia.

1.5.4.3 *Phlaeopterus cavicollis* (Fauvel, 1878)

Figs. 1.1C, 1.7A, 1.16C, 1.22B–1.22D, 1.28F

Type locality: British Columbia, Canada

1878 Fauvel: 246 [original description] original combination: *Tilea cavicollis*

1885 Casey: 320 as *Tilea cavicollis*

1893 Casey: 402 as *Tilea cavicollis*

1979 Moore and Legner: 208

1910 Bernhauer and Schubert: 74

1957 Hatch: 60

2001 Gandhi *et al.*: 139

2007 Hilchie: 2007

2015 Shavrin and Mullen: 121

= *brevipennis* Casey, 1893 **new synonym**

1893 Casey: 404 [original description] original combination: *Tilea brevipennis*

1957 Hatch: 60

= *longipalpus* Casey, 1885 **new synonym**

1866 LeConte: 375 [misidentification] as *P. fusconiger*

1885 Casey: 318 [original description] original combination: *Phloeopterus* [sic] *longipalpus*

1893 Casey: 402 as *Tilea longipalpus*

Habitus. (Fig. 1.1C) 6.3–9.2 mm in length. Brown to reddish-brown; elytra and lateral and basal margins of pronotum often lighter; palpi and elytral epipluerae sometimes lighter.

Head. Head broad, ratio of width across eyes to length of head about 5:4. Interantennal groove broadly and deeply impressed. Anteocellar foveae large, deeply impressed. Eye pubescence absent, or with less than 10 scattered setae near ventral margin. Antennae with segments 5–10 at least 2 times longer than wide; segments 4–11 each with many sensory pits with papilliform projections. Ocelli present. Nuchal constriction vague. Mandibles with molar area with L-shaped row of setae. Labrum with sensory pores along entire surface. Labial palpi with third segment 1.6–1.8 times longer than segment 2.

Thorax. Pronotum wide (Fig. 1.16C), length to width ratio = 0.61–0.68; ratio of width of pronotum to width of head = 1.49–1.72; maximum width subequal to elytra width at

humeral angle; punctures on dorsal surface separated by average distance equal to approximately twice as great as diameter of one puncture; lateral margins broadly explanate anterad and posterad the lateral foveae; lateral foveae deeply impressed. Elytra with humeral angles convex; epipleural carina not projecting; 2.2–2.7 times longer than pronotum; apical margins broadly convex to nearly truncate. Wings nearly always fully developed, rarely brachypterous. Mesosternum with projecting tooth, tooth more strongly notched on posterior margin than on anterior margin; longitudinal carina along midline of mesosternum complete.

Legs. Pro-, meso-, and metatibia with dense pubescence to apex or with small subglabrous region at apex. Metatrochanter without tooth on apical margin.

Abdomen. Wing-folding spicules on tergites IV and V broad, transverse, narrowly separated; tergite VI lacking wing-folding spicules.

Aedeagus. Somewhat variable (Figs. 1.22B–1.22D). 1.28–1.72 mm long. Median lobe convexly converging from base to midline, gradually converging from midline to apex. Parameres diverging from base to near apex, then converging towards apex of median lobe. Internal sac elongate, rectangular to narrowest near midline, subapical transverse fold present or absent.

Type specimens. Lectotype, male (UAMObs:Ento:235220), and paralectotype, female (UAMObs:Ento:232466), with label data as follows: Columbie

britannique/Syntype/LECTOTYPE ♂ (or PARALECTOTYPE ♀) *Tilea cavicollis* Fvl., desig. 1984 J.M. Campbell/*Phlaeopterus cavicollis* (Fvl.), det. 1984, J.M. Campbell. The paralectotype female is missing the Fauvel's handwritten determination label but otherwise has identical label data. Both specimens are in the RBINS, Brussels. Holotype, male (UAMObs:Ento:235786), with label data as follows: Wy/♂/CASEY bequest 1925/TYPE USNM 48109/brevipennis/HOLOTYPE ♂ Phlaeopterus brevipennis Casey. This specimen is in the USNM, Washington, DC. Lectotype, male (UAMObs:Ento:235764), with label data as follows: Oct.3/Placer Co. CAL./ ♂/T. longipalpus Cas./CASEY bequest 1925/TYPE USNM 48106/Lectotype ♂ Phlaeopterus longipalpus Casey des. 1984, J.M. Campbell. This specimen is in the USNM, Washington, DC.

Distribution. (Fig. 1.7A) *Phlaeopterus cavicollis* is widely distributed in western North America from southern California north though Coast Range and Cascade Range and the Rocky Mountains of British Columbia to southeastern Alaska, and east to Wyoming and Colorado. Adults have been collected from June–October, and in November in California, from 600–3500 m elevation. Adults have been observed feeding on wind-blown insects (mostly Diptera) on the surface of snowfields, breeding on the surface of snowfields, and rarely flying. Adults have also been collected under rocks at the edges of snowfields and in moss or under rocks at the edges of cold, fast streams or springs at lower elevations.

Remarks. *Phlaeopterus cavicollis* can be distinguished from all other *Phlaeopterus* species but *P. bakerensis* by having lateral margins of the pronotum broadly and subequally explanate anterad and posterad the lateral foveae. *Phlaeopterus cavicollis* can be

distinguished from *P. bakerensis* by its smaller size and by lacking projecting humeral angles of the elytra. We have chosen to synonymize *Phlaeopterus brevipennis* Casey and *Phlaeopterus longipalpus* Casey under *Phlaeopterus cavicollis* (Fauvel) **new synonymies** due to their shared characters (see description above), the presence of intermediate forms (discussed below), and their largely allopatric distributions.

The morphological variation that has previously been used to differentiate these three species is as follows: Specimens (previously *P. longipalpus*) from the Sierra Nevada and the Trinity Alps of California and Mt. Lassen, Nevada, have the tibiae evenly pubescent to the apex and the internal sac of the aedeagus roughly rectangular with a subapical transverse fold (Fig. 1.22D). Specimens (previously *P. cavicollis*) from Alaska, British Columbia, and the Coast and Cascade Ranges south to northern California usually also have the tibiae evenly pubescent to the apex and the internal sac of the aedeagus roughly triangular but lack a subapical transverse fold (Fig. 1.22B). Specimens (previously *P. brevipennis*) from the Rocky Mountains, Washington, Montana, and Colorado usually have the apex of the tibiae narrowly glabrous but sometimes evenly pubescent to the apex, and the internal sac of the aedeagus without a subapical transverse fold (Fig. 1.22C), and with margins narrowed near the midline. Some specimens intermediate between *P. cavicollis* and *P. brevipennis* from eastern Oregon, eastern Washington, and Idaho cannot be assigned to either name with certainty.

It is difficult to be certain whether these populations should be regarded as a single, broadly distributed, variable species or three distinct species. Given the available morphological evidence, we have chosen to regard them as a single species. Genetic

analysis would be useful in testing these synonymizations, but at present no sequence data is available for this species.

1.5.4.4 *Phlaeopterus czerskyi* (Shavrin)

Figs. 1.1D, 1.7B, 1.26, 1.30A–1.30E

Type locality: East Siberia, Russia

2001 Shavrin: 190 [original description] original combination: *Lesteva czerskyi*

2007 Shavrin, Shilenkov, and Anistschenko: 37 as *Lesteva czerskyi*

2015 Shavrin and Mullen: 121 [transferred to *Phlaeopterus*]

Habitus. (Fig. 1.1D) 4.0–4.3 mm in length. Dark brown to reddish brown; abdomen darkest; antennae, mouthparts, and legs often yellowish brown.

Head. Moderately wide, width across eyes greater than length. Interantennal groove vaguely impressed. Anteocellar foveae moderately impressed. Eyes moderately pubescent on ventral half, with more than 10 setae. Antennae with segments 5–10 1.2–1.8 times longer than wide. Ocelli present. Nuchal constriction vague. Mandibles with row of setae (Fig. 1.30B). Labrum with sensory pores along entire surface (Fig. 1.30A). Maxilla (Fig.

1.30D). Labial palpi with third segment greater than 2 times longer than second segment (1.30E).

Thorax. Pronotum moderately narrow, length to width ratio = 0.80; ratio of width of pronotum to width of head = 1.5; maximum width slightly less than width of elytra at base; dorsal surface very coarsely, sparsely punctate, punctures separated by average distance 1–2 times diameter of single puncture; lateral margins narrowly explanate posterad the lateral fovea, not explanate anterad the lateral foveae; lateral foveae vaguely impressed, contiguous with lateral margins. Elytra with humeral angles convex; epipleural carina not projecting; about 1.7 times longer than pronotum; apical margins convex. Wings brachypterous, reduced to short lobes. Mesosternum with projecting tooth; longitudinal carina along midline of mesosternum distinct, strongly and roughly carinate anteriorly, becoming vague posteriorly.

Legs. Pro-, meso-, and metatibia evenly pubescent to apex. Metatrochanter without tooth on apical margin.

Abdomen. Wing-folding spicules absent from all tergites. Apical palisade fringe on tergite VII absent.

Aedeagus. (Fig. 1.26) Median lobe somewhat triangular, apex acute. Parameres diverging from base to apical third, then slightly converging to apex. Internal sac heavily sclerotized, covered in microspinules.

Type specimens. Holotype, male, with label data as follows: 14.VI.[19]96/Хамар-Дабан [Khamar-Daban Mts.]/Комаринский [Komarinskiy]/хр. [Mt.] h=1900/ Øàâðèí À. [Shavrin A. leg.] Holotype/Lesteva/czerskyi/Shavrin A. 2000.

Paratype, female, with label data as follows: Хамар-Дабан [Khamar-Daban Mts.]/ ср. т. Бабхи [middle flow of Babkha River] [51º46' N, 103º95' E]/8–14.V.1999/ Шаврин А./[Shavrin A. leg.]/Paratype/Lesteva/czerskyi/Shavrin A. 2000. The holotype is deposited in ZIN, St. Petersburg, Russia. The paratype is deposited in CSH, Daugavpils, Latvia.

Distribution. (Fig. 1.7B) *Phlaeopterus czerskyi* is known only from the Khamar-Daban Mountains of East Siberia. Adults have been collected at 900–1900 m elevation from May–June in wet moss at the edges of small streams.

Remarks. *Phlaeopterus czerskyi* is the only species of the genus known outside of northwestern North America, and is easily distinguished from all other *Phlaeopterus* species by the crenulate lateral margins of the pronotum, the especially coarse and sparse punctation of the pronotum and elytra, the lack of wing-folding spicules, and the brachypterous wings. It most closely resembles *P. lagrandeuri*, and can be distinguished from *P. lagrandeuri* by characters discussed in the remarks section of that species. The occurrence of *P. czerskyi* in East Siberia confirms Casey's (1893) speculation: "[*Phlaeopterus*] is the most conspicuous of the endemic North American genera of Omaliini, although probably occurring also in Siberia…"

1.5.4.5 *Phlaeopterus elongatus* Campbell n. sp.

Figs. 1.2A, 1.8A, 1.17E, 1.17H, 1.20F, 1.25D, 1.29C, 1.32K–1.32L, 1.37F, 1.39E–1.39F, 1.40C, 1.41F

Type locality: Yoho National Park, British Columbia, Canada

Habitus. (Fig. 1.2A) 4.8–6.4 mm in length. Dark brown to black; tarsi, apex of tibiae, and antennae often lighter, reddish brown to dark brown.

Head. Head moderately narrow, ratio of width across eyes subequal to length of head (Fig. 1.59). Interantennal groove shallowly impressed. Anteocellar foveae large, deeply impressed. Eye pubescence absent, or with less than 10 scattered setae near ventral margin. Antennae with segments 5–10 at least 2 times longer than wide; segments 4–11 each with many sensory pits with papilliform projections (Fig. 1.37F). Ocelli present. Nuchal constriction vague. Mandibles with molar area with L-shaped row of setae (Fig. 1.29C). Maxilla (Figs. 1.32K–1.32L, 1.39E–1.39F). Hypopharynx (Fig. 1.40C). Labrum with sensory pores along entire surface. Labial palpi with third segment 1.6–1.8 times longer than segment 2.

Thorax. Pronotum narrow (Fig. 1.17E), length to width ratio = 0.88–0.95; ratio of width of pronotum to width of head = 1.27–1.41; maximum width less than width of elytra at base; punctures on dorsal surface separated by average distance slightly greater than diameter

of one puncture; without vague impression near midline on ventral surface (as in *P. filicornis*); lateral margins deflexed posterad and anterad the lateral foveae; lateral foveae vague, contiguous with and somewhat obscured by deflexed lateral margin. Elytra with humeral angles convex; epipleural carina not projecting; 2.4–2.7 times longer than pronotum; apical margins sexually dimorphic, broadly convex in males but somewhat prolonged at suture in females. Wings nearly always fully developed, rarely brachypterous. Mesosternum with projecting tooth; longitudinal carina along midline of mesosternum complete but vague (Fig. 1.20F).

Legs. Apex of pro-, meso-, and metatibia without pubescence, glabrous apex of metatibia length as ratio to metatibia length = 6.1–11.5. Metatrochanter without tooth on apical margin.

Abdomen. Wing-folding spicules on tergites IV and V broad, transverse, nearly contiguous; tergite VI with small, nearly circular wing-folding patches (Fig. 1.17H).

Aedeagus. (Fig. 1.25D) 0.90–1.05 mm long. Median lobe triangular; apex somewhat acute. Parameres nearly straight. Internal sac expanded at base; moderately sclerotized; evenly covered in microspinules.

Type specimens. Holotype, male (UAMObs:Ento:235834), and allotype, female (UAMObs:Ento:235835), with label data as follows: Alta., 20 mi. SW Kananaskis F.E.S. [Forest Experiment Station], 7000', Snow Ridge, VII-31-1971, J.M. & B.A.

Campbell/Holotype ♂ (or Allotype ♀) Phlaeopterus elongatus, desig. 1984, J.M. Campbell, CNC No. 18462. Both specimens are deposited in the CNC, Ottawa. Paratypes: 122, deposited in the AMNH, CAS, CSCA, CNC, FMNH, MCZ, and USNM.

Distribution. (Fig. 1.8A) *Phlaeopterus elongatus* is known from the Rocky Mountains from Wyoming north to Summit Lake, British Columbia, in the Cascade Range and Selkirk Mountains of British Columbia, and the Alaska Range and Talkeetna Mountains of Alaska. Adults have been collected at 1100–3200 m elevation during June–September from particularly cold habitats including the edges of snowfields, lakes fed by melting snow, and sometimes from wet moss in the splash zones of waterfalls or the edges of streams. Unlike other new species described herein that have not been re-collected since the late 1970s or early 1980s, we have collected *P. elongatus* extensively in the Alaska Range and Talkeetna Mountains during the summers of 2013–2014, suggesting these populations are thriving in Alaska.

Remarks. *Phlaeopterus elongatus* can be distinguished from all other *Phlaeopterus* species by its elongate form, its especially narrow pronotum, and the presence of wing-folding spicules on tergite VI. This species has been misidentified as *P. filicornis* in most collections but can be differentiated from *P. filicornis* by the aforementioned characters as well as its smaller size, darker color, shallower interantennal groove, longer glabrous region of the mesotibia, and aedeagus with median lobe narrower.

Etymology. The name of this species is derived from the Latin *elongate*, referring to the particularly elongate shape of the body.

1.5.4.6 *Phlaeopterus filicornis* Casey

Figs. 1.2B, 1.8B, 1.17C, 1.25B, 1.29G, 1.31H

Type locality: Placer County, California, USA

1883 Casey: 403 [original description] original combination: *Tilea filicornis*

1886 Casey: 234

1985 Elias: 38

= *rufitarsis* Casey, 1883 **new synonym**

1883 Casey: 403 [original description] original combination: *Tilea rufitarsis*

Habitus. (Fig. 1.2B) 5.9–7.7 mm in length. Dark brown, almost black, palpi, elytra, glabrous apices of tibiae lighter.

Head. Head moderately narrow, ratio of width across eyes subequal to length of head. Interantennal groove deeply impressed. Anteocellar foveae large, deeply impressed. Eye pubescence absent, or with less than 10 scattered setae near ventral margin. Antennae

with segments 5–10 at least 2 times longer than wide; segments 4–11 each with many sensory pits with papilliform projections. Ocelli present. Nuchal constriction vague. Mandibles with molar area with L-shaped row of setae. Labrum with sensory pores along entire surface (Fig. 1.31H). Labial palpi with third segment 1.6–1.8 times longer than segment 2.

Thorax. Pronotum moderately narrow (Fig. 1.17C), length to width ratio = 0.76–0.81; ratio of width of pronotum to width of head = 1.35–1.43; maximum width less than width of elytra at base; punctures on dorsal surface separated by average distance equal to greater than diameter of single puncture; with vague impression near midline on ventral surface; lateral margins deflexed posterad and anterad the lateral foveae; lateral foveae moderately impressed. Elytra with humeral angles convex; epipleural carina not projecting; 2.4–3.2 times longer than pronotum; apical margins sexually dimorphic, elongated at suture and slightly diverging in females (Fig. 1.29G) and broadly convex and not diverging in males. Wings nearly always fully developed, rarely brachypterous. Mesosternum with projecting tooth; longitudinal carina along midline of mesosternum complete.

Legs. Apex of pro-, meso-, and metatibia without pubescence, subglabrous apex of metatibia length as ratio to metatibia length = 4.9–8.8. Metatrochanter without tooth on apical margin.

Abdomen. Wing-folding spicules on tergites IV and V broad, transverse, nearly contiguous; tergite VI lacking wing-folding patches.

Aedeagus. (Fig. 1.25C) 1.25–1.38 mm long. Median lobe somewhat triangular, apex acutely triangular. Parameres diverging from base until just before apex. Internal sac elongate, lightly sclerotized, evenly covered in small microspinules.

Type specimens. Lectotype male (UAMObs:Ento:235784), with label data as follows: Sept./Placer Co. Cal./ ♂/CASEY bequest 1925/TYPE USNM 48108/filicornis Casey/LECTOTYPE ♂ Tilea filicornis Csy. des. 1982, J.M. Campbell. Paralectotype male (UAMObs:Ento:235785) with label data as follows: Sept./Placer Co. Cal./ CASEY bequest 1925/CASEY det. 2 filicornis/ PARALECTOTYPE ♂ Tilea filicornis Csy., des. 1982, J.M. Campbell. Lectotype male, Siskiyou Co. Cal./ ♂/CASEY bequest 1925/TYPE USNM 48107/rufitarsis/LECTOTYPE ♂ Tilea rufitarsis Csy. des. 1982, J.M. Campbell. All four specimens are deposited in the USNM, Washington, DC.

Distribution. (Fig. 1.8B) *Phlaeopterus filicornis* is known only from California in the Sierra Nevada and Cascade Range. Adults have been collected from 1820–3440 m elevation from July–September under rocks near cold, fast-flowing streams or at the edges of permanent or long-lasting snowfields, and in moss at the edges of streams or in the splash zones of waterfalls.

Remarks. *Phlaeopterus filicornis* can be distinguished from all other species by the shape of the pronotum, sexually dimorphic shape of the apex of the elytra, glabrous apices of the tibiae, and aedeagus. It is highly similar to *P. hatchi*, from which it differs by the sexually

dimorphic shape of the apex of the elytra, pronotum with vague impression near midline on ventral surface, shape and size of the median lobe of the aedeagus, microspinules of the internal sac of the aedeagus, and a slight difference in body length. These two species formed an intermixed clade in Chapter 2, but this may be an artifact of short COI sequence length/missing data. *Phlaeopterus filicornis* and *P. hatchi* are allopatric, but are sufficiently morphologically distinct to be regarded as separate species.

We have examined the holotypes of *P. filicornis* and *P. rufitarsus* and were not able to find any significant differences in the two specimens. We have therefore chosen to synonymize *P. rufitarsis* under *P. filicornis,* **new synonymy**.

1.5.4.7 *Phlaeopterus frosti* Hatch

Figs. 1.2C, 1.9A, 1.17B, 1.20D, 1.25A, 1.36D

Type locality: Mt. Rainier, Washington, USA

1957 Hatch: 59 [original description]

1991 Campbell and Davies: 5

Habitus. (Fig. 1.2C) 5.8–7.2 mm in length. Reddish-brown to black; legs, elytral epipleura, tarsi, and apices of tibiae lighter reddish-brown to yellowish-brown.

Head. Head slightly broader than long, ratio of width across eyes to length of head = 4:3. Interantennal groove broadly and deeply impressed. Anteocellar foveae large, deeply impressed. Eye pubescence absent, or with less than 10 scattered hairs near ventral margin (Fig. 1.36D). Antennae with segments 5–10 at least 2 times longer than wide; segments 4–11 each with many sensory pits with papilliform projections. Ocelli present. Nuchal constriction vague. Mandibles with molar area with L-shaped row of setae. Labrum with sensory pores along entire surface. Labial palpi with third segment 1.6–1.8 times longer than segment 2.

Thorax. Pronotum moderately wide (Fig. 1.17B), length to width ratio = 0.68–0.72; ratio of width of pronotum to width of head = 1.54–1.67; maximum width subequal to elytra width at humeral angle; punctures separated by distance equal to slightly greater than diameter of one puncture; lateral margins explanate posterad but not anterad the lateral foveae; lateral foveae deeply impressed. Elytra with humeral angles convex; epipleural carina not projecting; 2.1–2.2 times longer than pronotum; apical margins convex or subtruncate. Wings nearly always fully developed, rarely brachypterous. Mesosternum with projecting tooth; longitudinal carina along midline of mesosternum distinct on anterior half, distinct or reduced on posterior half (Fig. 1.20D).

Legs. Apex of pro-, meso-, and metatibia without pubescence, subglabrous apex of mesotibia subequal to length of basal four tarsal segments (Fig. 1.18A), subglabrous apical region of metatibia length as ratio to metatibia length in males = 4.9–8.4, in females = 4.2–5.5. Metatrochanter without tooth on apical margin.

Abdomen. Wing-folding spicules on tergites IV and V; shape of wing-folding patches on tergite V broadly oval and narrowly separate.

Aedeagus. (Fig. 1.25A) 1.23–1.40 mm long. Median lobe somewhat triangular with sides narrowing from base to apex; apex not carinate. Parameres extending slightly beyond apex of median lobe. Internal sac rectangular and elongate; heavily sclerotized, uniformly covered with microspinules; lacking subapical transverse fold.

Types. Holotype male (UAMObs:Ento:235778), and allotype female (UAMObs:Ento:235779), each with labels as follows: Mt. Rainier, WASH., below Sluskin Falls, Aug. 23, 1930 M.H. Hatch TYPE ♂ (or ALLOTYPE ♀), Phlaeopterus frosti, 1951–M.H. Hatch. Both specimens are deposited in the USNM.

Distribution. (Fig. 1.9A) *Phlaeopterus frosti* is found in the Cascade Range from Oregon north to Manning Provincial Park, British Columbia, in the Olympic Mountains of Washington, in the Coast Range, Selkirk Mountains, and southern Rocky Mountains of British Columbia, and in the Kenai Mountains of Alaska. Adults have been collected at 50–2050 m elevation from June–August. This species has been collected on the surface of permanent or long-lasting snowfields at night in Washington and Oregon where they forage immediately after dusk, and during the day in British Columbia. They have also been collected under rocks at the edges of snowfields and cold, fast-flowing streams, in moss growing in the splash-zones of waterfalls, and occasionally in the gravelly, marshy edges of

high elevation lakes. On the surface of snowfields, they have been observed feeding on small insects (mostly Diptera) stranded on the surface of the snow.

Remarks. *Phlaeopterus frosti* can be distinguished from all other *Phlaeopterus* species by the shape of the pronotum, the glabrous region at the apex of the tibiae, and the aedeagus. This species is very similar to *P. fusconiger*, but can be distinguished by the characters discussed in the remarks section of the latter species. These two species are sympatric in the Coast Range from the Olympic Mountains of Washington north to the Kenai Mountains of Alaska.

1.5.4.8 *Phlaeopterus fusconiger* Motschulsky

Figs. 1.3C, 1.9B, 1.17A, 1.18B, 1.24D

Type locality: Unalaska Island, Alaska, USA

1853 Motschulsky: 78 [original description]

1853 Mäklin: 193 as *Lesteva fusconigra*

1878 Fauvel: 248 as *Lesteva fusconigra*

1885 Casey: 320 as *Phloeopterus* [sic] *fusconiger*

1893 Casey: 402 as *Tilea fusconigra*

1952 Blackwelder: 303

1966 Moore: 52

1979 Moore and Legner: 193

1991 Campbell and Davies: 5

2001 Herman: 366

2015 Shavrin and Mullen: 121

Habitus. (Fig. 1.3C) 5.8–7.2 mm in length. Dark brown to reddish-brown; legs, elytral epipleura, and tarsi often lighter; apices of tibiae, tarsi, and palpi even lighter reddish-brown; elytra usually slightly lighter than pronotum.

Head. Head slightly broader than long, ratio of width across eyes to length of head = 4:3. Interantennal groove broadly and deeply impressed. Anteocellar foveae large, deeply impressed. Eye pubescence absent, or with less than 10 scattered setae near ventral margin. Antennae with segments 5–10 at least 2 times longer than wide; segments 4–11 each with many sensory pits with papilliform projections. Ocelli present. Nuchal constriction vague. Mandibles with molar area with L-shaped row of setae. Labrum with sensory pores along entire surface. Labial palpi with third segment 1.6–1.8 times longer than segment 2.

Thorax. Pronotum moderately wide (Fig. 1.17A), length to width ratio = 0.68–0.72; ratio of width of pronotum to width of head = 1.54–1.67; maximum width subequal to elytra width at humeral angle; punctures separated by distance equal to slightly greater than diameter of one puncture; lateral margins explanate posterad but not anterad the lateral foveae;

lateral foveae deeply impressed. Elytra with humeral angles convex; epipleural carina not projecting; 2.1–2.2 times longer than pronotum; apical margins convex or subtruncate. Wings nearly always fully developed, rarely brachypterous. Mesosternum with projecting tooth, tooth more strongly notched on posterior margin than on anterior margin; longitudinal carina along midline of mesosternum distinct on anterior half, reduced on posterior half.

Legs. Apex of pro-, meso-, and metatibia without pubescence, subglabrous apex of mesotibia subequal to length of basal three tarsal segments (Fig. 1.18B), glabrous apical region of metatibia length as ratio to metatibia length in males = 7.4–12.2, in females = 6.6–8.6. Metatrochanter without tooth on apical margin.

Abdomen. Wing-folding spicules on tergites IV and V; shape of wing-folding patches on tergite V broadly oval and narrowly separate.

Aedeagus. (Fig. 1.24D) 1.23–1.43 mm long. Median lobe with margins concavely constricted near midline. Parameres convex, converging past apex of median lobe. Internal sac rectangular; lightly sclerotized, uniformly covered with microspinules; lacking subapical transverse fold.

Type specimen. Holotype female (UAMObs:Ento:235794), with labels as follows: Unalaschka, Phlaeopterus fusconiger Motsch., Unalaschka [Unalaska Island]/Phlaeopterus fusconiger Mots., HOLOTYPE, exam. 1984 J.M. Campbell.

As of 1984 the holotype was confirmed by J.M. Campbell to be located in the collection of the Zoological Museum, University of Moscow, Russia. The specimen is glued to a transparent plate and badly damaged with both elytra and apical five segments of right antenna, right middle and hind legs, and apical four segments of the metatarsus missing. In 2015, A.V. Shavrin visited the collection and could not locate the holotype, reporting that Motschulsky's collection was badly damaged by dermestids and fungi. Although the holotype is possibly missing, this species is currently in no danger of being confused with similar species, thus a neotype is not needed.

Distribution. (Fig. 1.9B) *Phlaeopterus fusconiger* is widely distributed along the northwest coast of North America, from the Olympic Mountains of Washington north through the Coast Range, on Vancouver Island and the Haida Gwaii, to the Aleutian Islands and Nome, Alaska. Adults have been collected at near sea level in Alaska up to 2000 m in mainland Washington and British Columbia from June–August. The Nome record (UAMObs:Ento:234463) is the northern-most record for any *Phlaeopterus* species.

Remarks. *Phlaeopterus fusconiger* can be distinguished from all other *Phlaeopterus* species by the shape of the pronotum, the glabrous region at the apex of the tibiae, and the aedeagus. This species is very similar to *P. frosti*, but can be distinguished by the shorter glabrous region of the mesotibia, slightly lighter color, more strongly developed anterior margins of the mesosternal notch, and by the aedeagus with the internal sac shorter, broader, less heavily sclerotized, and with the apex less acutely narrowed. These two

species are sympatric in the coast range from the Olympic Mountains of Washington north to the Kenai Mountains of Alaska. We have confirmed the surprising occurrence of *P. fusconiger* in Nome, Alaska by examination of a single specimen collected in Nome by George Ball in 1958 (UAMObs:Ento:234463). However, we are aware of no additional specimens of *Phlaeopterus* from Nome, or anywhere on the Seward Peninsula. This remote population would be interesting to confirm and compare genetically to other populations of this species.

1.5.4.9 *Phlaeopterus hatchi* Campbell n. sp.

Figs. 1.3A, 1.10A, 1.17D, 1.25B, 1.29F, 1.35C–1.35D

Type locality: Mt. Begbie, British Columbia, Canada

1957 Hatch: 59 [misidentification] as *Phlaeopterus rufitarsis*

Habitus. (Fig. 1.3A) 5.5–6.9 mm in length. Dark brown, almost black; palpi, elytra, and glabrous apices of tibiae lighter.

Head. Head moderately narrow, ratio of width across eyes subequal to length of head. Interantennal groove shallowly impressed (Fig. 1.35C–1.35D). Anteocellar foveae large, deeply impressed. Eye pubescence absent, or with less than 10 scattered setae near ventral

margin. Antennae with segments 5–10 at least 2 times longer than wide; segments 4–11 each with many sensory pits with papilliform projections. Ocelli present. Nuchal constriction vague. Mandibles with molar area with L-shaped row of setae. Labrum with sensory pores along entire surface. Labial palpi with third segment 1.6–1.8 times longer than segment 2.

Thorax. Pronotum moderately narrow (Fig. 1.17D), length to width ratio = 0.78–0.84; ratio of width of pronotum to width of head = 1.30–1.39; maximum width less than width of elytra at base; punctures on dorsal surface separated by average distance equal to greater than diameter of single puncture; without vague impression near midline on ventral surface (as in *P. filicornis*); lateral margins deflexed posterad and anterad the lateral foveae; lateral foveae moderately impressed. Elytra with humeral angles convex; epipleural carina not projecting; 2.4–3.0 times longer than pronotum; apical margins not sexually dimorphic, broadly convex and not diverging in both sexes (Fig. 1.29F). Wings nearly always fully developed, rarely brachypterous. Mesosternum with projecting tooth; longitudinal carina along midline of mesosternum complete.

Legs. Apex of pro-, meso-, and metatibia without pubescence, subglabrous apex of metatibia length as ratio to metatibia length = 4.4–7.8. Metatrochanter without tooth on apical margin.

Abdomen. Wing-folding spicules on tergites IV and V broad, transverse, nearly contiguous; tergite VI lacking wing-folding patches.

Aedeagus. (Fig. 1.25B) 1.28–1.40 mm long. Median lobe short, with lateral margins subparallel then acutely triangular nearing apex. Internal sac elongate, nearly as long as median lobe, moderately heavily sclerotized, covered in microspinules with distinctly larger microspinules in patches near apex.

Type specimens. Holotype male (UAMObs:Ento:235832), and allotype female (UAMObs:Ento:235833), with label data as follows: B.C., Mt. Begbie, 6300', VIII–30–1971, J.M. Campbell/ HOLOTYPE ♂ (or ALLOTYPE ♀) Phlaeopterus hatchi, desig. 1984, J.M. Campbell, CNC No. 18463. Both specimens are deposited in the CNC, Ottawa. Paratypes: 73, deposited in the AMNH, CAS, CSCA, CNC, FMNH, MCZ, and USNM.

Distribution. (Fig. 1.10A) *Phlaeopterus hatchi* is known from northern California north through the Cascade Range, the Mission Mountains of Montana, the Rocky Mountains of British Columbia, and in Alaska by a single specimen (UAMObs:Ento:232742) collected by A. Ord in 2012 between Haines and Juneau. Adults have been collected at 1100–2130 m elevation from July–August. Adults were mostly collected from under stones at the edges of small, cold streams, but sometimes were taken under rocks near snowfields or in splash zones of waterfalls and moss along the edges of streams.

Remarks. *Phlaeopterus hatchi* can be distinguished from all other *Phlaeopterus* species by the shape of the pronotum, glabrous apices of the tibiae, and the aedeagus. It is similar to *P.*

filicornis, from which it differs by characters discussed in the remarks section of that species.

Etymology. This species was named in honor of Dr. Melville H. Hatch.

1.5.4.10 *Phlaeopterus houkae* Hatch

Figs. 1.4B, 1.10B, 1.15F, 1.17F, 1.19F, 1.21B, 1.28F, 1.31F, 1.32G–1.32H, 1.33F, 1.34C–1.34D, 1.37D, 1.36B, 1.39A–1.39B, 1.40F, 1.42D

Type locality: Mt. Baker, Washington, USA

1957 Hatch: 58 [original description]

1991 Campbell and Davies: 5

2001 Herman: 377

Habitus. (Fig. 1.4B) Dark brown; elytra usually lighter; legs, antennae, and mouthparts yellowish brown; abdomen usually reddish brown.

Head. Width moderate, width across eyes slightly wider than long (Fig. 1.34C–1.34D). Interantennal groove vague or absent at least across midline of head. Anteocellar foveae vague, shallowly impressed. Eyes moderately pubescent on ventral half, with more than 10

setae (Fig. 1.36B). Antennae with segments 3–10 each 1.6–2.0 times longer than wide; segments 4–11 each with many sensory pits with papilliform projections (Fig. 1.37D). Ocelli present. Nuchal constriction absent. Epipharynx (Fig. 1.33F). Hypopharynx (Fig. 1.40F). Mandibles with molar area with L-shaped row of setae (Fig. 28F). Labrum with sensory pores along anterior margin only (Fig. 1.31F). Maxilla with lacinia and galea (Figs. 1.32G–1.32H , 1.39A–1.39B). Labial palpi with third segment 1.2–1.5 times longer than second segment (Fig. 1.42D).

Thorax. Pronotum narrow (Fig. 1.15F), length to width ratio = 0.7–0.8; ratio of width of pronotum to width of head = 1.3–1.4; maximum width subequal to width of elytra at base; punctures separated by average distance equal to to slightly less than diameter of one puncture; lateral margins narrowly explanate posterad the lateral fovea, not explanate anterad the lateral foveae; lateral foveae moderately impressed, contiguous with lateral margins. Elytra with humeral angles convex; epipleural carina not projecting; 1.9–2.1 times longer than pronotum; apical margins convex. Wings brachypterous. Mesosternum with projecting tooth; longitudinal carina along midline of mesosternum present but vague, especially near midline and posterior margin (Fig. 1.19F).

Legs. Pro-, meso-, and metatibia evenly pubescent to apex. Metatrochanter without tooth on apical margin.

Abdomen. Tergites IV and V each with wing folding spicules very broad, nearly contiguous or contiguous in shape of single transverse band (Fig. 1.17F). Apical palisade fringe on tergite VII absent.

Aedeagus. (Fig. 1.21B) 0.65–0.75 mm long. Median lobe with lateral margins subparallel from base to past midline, then abruptly narrowed, apex acute. Parameres broad; parallel and nearly straight. Internal sac with two dense patches of spicules lateroapically.

Type specimen. Holotype, female (UAMObs:Ento:235216), with label data as follows: Mt. Baker Lodge, Aug. 26, 1935, WASH., M.H. Hatch/Det. 1954, H. Houk/not Vellica longipennis Csy., compared with type, M.H. Hatch 1958/TYPE ♀ Phlaeopterus houkae 1951 – M.H. Hatch/Vellica longipennis Csy., compared with Fall coll., M.H. Hatch 1952. The specimen is deposited in the USNM, Washington DC.

Distribution. (Fig. 1.10B) *Phlaeopterus houkae* is known broadly from the Coast Range and Cascade Range, from Siskiyou County, California and Oregon north to the Alaska Range in Alaska. It is also known coastally from Baranof Island, Prince of Whales Island, the Haida Gwaii, Vancouver Island, and the Olympic Mountains. Adults have been collected at 90–2400 m elevation from June–August in wet moss at the edge of cold water, usually small streams and pools.

Remarks. *Phlaeopterus houkae* can be distinguished from all other *Phlaeopterus* species by its small size, presence of ocelli, vague anteocellar foveae, slight nuchal constriction, shape

and punctation of the pronotum, shape of the wing folding spicules on tergites IV and V, lack of wing folding spicules on tergite VI, and the unique structure of the internal sac of the aedeagus.

1.5.4.11 *Phlaeopterus kavanaughi* Campbell n. sp.

Figs. 1.3C, 1.11A, 1.16A, 1.21E, 1.35A–1.35B, 1.40B

Type locality: Lassen National Park, California, USA

Habitus. (Fig. 1.3C) 6.2–7.6 mm in length. Dark brown to reddish brown to yellowish brown; head and abdomen nearly black, elytra usually distinctly lighter reddish to yellowish brown; margins of pronotum often also distinctly lighter reddish brown to yellowish brown; palpi, antennae, and legs reddish brown to yellowish brown.

Head. Head moderately broad (Fig. 1.35A–1.35B), ratio of width across eyes to length of head = 1.0–1.3. Interantennal groove broadly and deeply impressed. Anteocellar foveae large, deeply impressed. Eye pubescence absent, or with less than 10 scattered setae near ventral margin. Antennae with segments 5–10 at least 2 times longer than wide; segments 4–11 each with many sensory pits with papilliform projections. Ocelli present. Nuchal constriction vague. Mandibles with molar area with L-shaped row of setae. Hypopharynx

(Fig. 1.40B). Labrum with sensory pores along entire surface. Labial palpi with third segment 1.6–1.8 times longer than second segment.

Thorax. Pronotum broad (Fig. 1.16A), length to width ratio = 0.71–0.79; ratio of width of pronotum to width of head = 1.49–1.67; maximum width subequal to elytra width at humeral angle; punctures on dorsal surface separated by average distance slightly greater than diameter of single puncture; lateral margins explanate posterad the lateral foveae, not explanate anterad the lateral foveae; lateral foveae deeply impressed. Elytra with humeral angles convex; epipleural carina not projecting; 2.1–2.6 times longer than pronotum. Wings nearly always fully developed, rarely brachypterous. Mesosternum with projecting tooth; longitudinal carina along midline of mesosternum complete but not strongly carinate.

Legs. Pro-, meso-, and metatibia with dense pubescence from base to apex. Metatrochanter without tooth on apical margin.

Abdomen. Wing-folding spicules on tergites IV and V broad, transverse, narrowly separated; tergite VI lacking wing-folding patches.

Aedeagus. (Fig. 1.21E) 1.16–1.34 mm long. Median lobe approximately evenly, somewhat convexly narrowed from base to apex; with vague ventral longitudinal carina at apex. Parameres narrow. Internal sac elongate, tube-like, moderately sclerotized; with distinct median transverse fold.

Primary types. Holotype male (UAMObs:Ento:235218), and allotype female (UAMObs:Ento:235831), with label data as follows: CAL. Lassen N. P., base of Summit Tr., 8500', 16.VII.1979, JM & BA Campbell/HOLOTYPE ♂ (or ALLOTYPE ♀) *Phlaeopterus kavanaughi*, desig. 1984, J.M. Campbell, CNC No. 18464. Both specimens are deposited in the CNC, Ottawa. Paratypes: 183, deposited in AMNH, NHMUK, CAS, CSCA, FMNH, MCZ, OSAC, USNM, UCRC.

Distribution. (Fig. 1.11A) *Phlaeopterus kavanaughi* is known from Sierra Nevada and Cascade Range of California north to Oregon. Adults have been collected from July–August at 1830–3400 m elevation, with a single specimen (UAMObs:Ento:234158) collected at 90 m in Multnomah County, Oregon. This species has been collected at night on snowfields where they have been observed feeding on windblown arthropods on the surface of the snow.

Remarks. *Phlaeopterus kavanaughi* can be distinguished from all other *Phlaeopterus* species by the tibiae pubescent to apices, the shape of the lateral margins of the pronotum, the ventral longitudinal carina of the median lobe of the aedeagus, the shape and median transverse fold of the internal sac of the aedeagus, and usually the yellowish brown elytra and lateral margins of the pronotum, lighter than remainder of habitus.

Etymology. This species is named in honor of Dr. D.H. Kavanaugh, California Academy of Sciences, San Francisco, California, USA.

1.5.4.12 *Phlaeopterus lagrandeuri* Hatch

Figs. 1.3D, 1.11B, 1.15E, 1.19E, 1.21A, 1.28E, 1.31E, 1.32E–1.32F, 1.33E, 1.34A–1.34B, 1.36A, 1.38E–1.38F, 1.40E, 1.41D

Type locality: Carkeek Park, Seattle, Washington, USA

1957 Hatch: 58 [original description]

1991 Campbell and Davies: 5

2001 Herman: 377

2015 Shavrin and Mullen: 121

Habitus. (Fig. 1.3B) 3.5–4.7 mm long. Dark brown to reddish brown; legs, mouthparts, antennae, and elytra usually lighter; elytra with distinctive yellow to reddish-yellow area, ranging from small spot on humeri to nearly covering elytral disc.

Head. Moderately narrow, width across eyes slightly wider than long (Figs. 1.34A–1.34B). Interantennal groove large, deeply impressed. Anteocellar foveae small, shallowly impressed. Eyes moderately pubescent on ventral half, with more than 10 setae (Fig. 1.36A). Antennae with segments 5–10 1.2–1.8 times longer than wide; segments 4–11 each with many sensory pits with papilliform projections. Ocelli present. Nuchal constriction vague. Mandibles with molar area with L-shaped row of setae and additional oblique row of

setae (Fig. 1.28E). Labrum with sensory pores along anterior margin only (Fig. 1.31E). Maxilla with lacinia and galea (Figs. 1.32E–1.32F, 1.38E–1.38F). Epipharynx (Fig. 1.33E). Hypopharynx (Fig. 1.40E). Labial palpi with third segment 1.1–1.3 times longer than second segment.

Thorax. Pronotum moderately narrow (Fig. 1.15E), length to width ratio = 0.68–0.72; ratio of width of pronotum to width of head = 1.54–1.67; maximum width less than width of elytra at base; dorsal surface coarsely, sparsely punctate, punctures separated by average distance slightly less than diameter of one puncture; lateral margins narrowly explanate posterad the lateral fovea, not explanate anterad the lateral foveae; lateral foveae moderately impressed, contiguous with lateral margins. Elytra with humeral angles convex; epipleural carina not projecting; 2.2–2.5 times longer than pronotum; apical margins convex. Wings fully developed. Mesosternum with projecting tooth; longitudinal carina along midline of mesosternum absent or vague.

Legs. Pro-, meso-, and metatibia evenly pubescent to apex. Metatrochanter with tooth on apical margin (Fig. 1.41D). Protibiae slightly sinuate on medioventral margin in males.

Abdomen. Wing-folding spicules on tergites IV and V broad, transverse, nearly contiguous; tergite VI without wing-folding spicules. Apical palisade fringe on tergite VII absent.

Aedeagus. (Fig. 1.21A) 0.63–0.70 mm long. Median lobe triangular. Parameres broad, diverging until just past midline then converging towards apex of median lobe. Internal sac irregular in shape; with two apical patches of thick setae.

Type specimens. Holotype, male (UAMObs:Ento:235215), with label data as follows: Seattle, WASH., Carkeek Park, Bel., V.3.1949/Type ♂, Phlaeopterus lagrandeuri, 1951, M.H. Hatch. Allotype, female (UAMObs:Ento:235775), with label data as follows: Corvallis, ORE., VI.1.1946, KM & DM Fender/ALLOTYPE ♀ Phlaeopterus lagrandeuri 1951, M.H. Hatch/Marys Peak. Both specimens are deposited in the USNM, Washington DC.

Distribution. (Fig. 1.11B) *Phlaeopterus lagrandeuri* is widely distributed from the Kenai Peninsula of Alaska, British Columbia, including the Haida Gwaii and Vancouver Island, south through Washington and Oregon, and from Calahan, California with one specimen (UAMObs:Ento:232633). Adults have been collected from near sea level at the coast to 2200 m elevation during May–August.

Remarks. *Phlaeopterus lagrandeuri* is easily distinguished from all other *Phlaeopterus* species by the especially coarse, sparse punctation of the pronotum and elytra, yellow spot on each elytron (although occasionally vague or absent), tooth on the apical margin of the metatrochanter, mandibles, and unique structure of the internal sac of the aedeagus. This species most closely resembles *P. czerskyi* but can be distinguished by many characters including the more shallowly impressed anteocellar foveae, less coarse punctation, lateral margins of pronotum smooth, not crenulate, fully developed wings, and shorter elytra.

Phlaeopterus lagrandeuri is known only from North America while *P. czerskyi* is known only from Siberia.

1.5.4.13 *Phlaeopterus loganensis* Hatch

Figs. 1.4A, 1.29E, 1.16H, 1.24C, 1.12A

Type locality: Logan Pass, Glacier National Park, Montana, USA

1957 Hatch: 60 [original description]

1991 Campbell and Davies: 5

Habitus. (Figs. 1.4A) 5.8–7.4 mm in length. Dark-brown to black; head often black, pronotum and elytra lighter; antennae, palpi, and legs even lighter, legs becoming progressively lighter from base to apex.

Head. Width across eyes to length of head subequal to slightly wider than long. Interantennal groove broadly and shallowly impressed. Anteocellar foveae large, deeply impressed. Eye pubescence absent, or with less than 10 scattered setae near ventral margin. Antennae with segments 5–10 at least 2 times longer than wide; segments 4–11 each with many sensory pits with papilliform projections. Ocelli present. Nuchal constriction vague. Mandibles with molar area with L-shaped row of setae. Labrum with

sensory pores along entire surface. Labial palpi with third segment 1.6–1.8 times longer than segment 2.

Thorax. Pronotum moderately wide (Fig. 1.16H), length to width ratio = 0.68–0.75; ratio of width of pronotum to width of head = 1.52–1.67; maximum width subequal to elytra width at humeral angle; punctures separated by distance slightly less than diameter of one puncture on center of disc, almost contiguous towards margin; lateral margins explanate posterad but not anterad the lateral foveae; lateral foveae deeply impressed. Elytra with humeral angles convex; epipleural carina not projecting; 2.2–2.7 times longer than pronotum; apical margins broadly triangular, elongated at suture (Fig. 1.29E). Wings nearly always fully developed, rarely brachypterous. Mesosternum with projecting tooth; longitudinal carina along midline of mesosternum indistinct.

Legs. Apex of pro-, meso-, and metatibia without pubescence, subglabrous apex of metatibia length as ratio to metatibia length in males = 10.2–17.3, in females = 8.1–13.0. Metatrochanter without tooth on apical margin.

Abdomen. Wing-folding spicules on tergites IV and V broad, narrowly separated; wing-folding patches on tergite VI small, circular to slightly transverse. Apical palisade fringe on tergite VII present.

Aedeagus. (Fig. 1.24C) 1.4–1.55 mm long. Median lobe narrow, elongate, lateral margins constricted and subparallel near midline, expanding anterad and posterad the midline.

Parameres narrow, convexly curved. Internal sac elongate, lightly sclerotized, dorsal half evenly, lightly covered in microspinules.

Type specimens. Holotype male (UAMObs:Ento:235773), and allotype female (UAMObs:Ento:235774), each with labels as follows: G.N.P. Mont., Logan Pass, Aug. 22, 1939, M.H. Hatch/ TYPE ♂ (or ALLOTYPE ♀), *Phlaeopterus loganensis*, 1951–M.H. Hatch. Both specimens are deposited in the USNM, Washington, DC.

Distribution. (Fig. 1.12A) *Phlaeopterus loganensis* is known only from the Rocky Mountains of Idaho, Montana, and British Columbia, the Selkirk Mountains of British Columbia, and Banff and Jasper National Parks, Alberta. Adults have been collected from June–September at 600–2400 m elevation in wet moss and piles of rocks at the edges of fast, cold streams, in the splash-zone of waterfalls and cascades, and under rocks at the edges of snowfields or snowmelt ponds. Specimens collected at low elevations were associated with springs or fast streams, which remain cold to lower elevations.

Remarks. *Phlaeopterus loganensis* can be distinguished from all other *Phlaeopterus* species by having the apex of the elytra triangular in both males and females (Fig. 1.29E). Although *P. elongatus* and *P. filicornis* have the apex of the elytra triangular in females, no other species of the genus have the apex of the elytra triangular in both sexes. *Phlaeopterus loganensis* is most similar to *P. olympicus*, and these two species can be distinguished by characters discussed in the remarks section of the latter species.

1.5.4.14 *Phlaeopterus longipennis* (Casey) new combination

Fig. 1.4B, 1.12B, 1.15G, 1.20A, 1.21C, 1.32C, 1.36C, 1.41E

Type locality: Placer County, California, USA

1885 Casey: 321 [original description] original combination: *Vellica longipennis*

1893 Casey: 401 as *Vellica longipennis*

1966 Moore: 52 as *Vellica longipennis*

1979 Moore and Legner: 199 as *Vellica longipennis*

1991 Campbell and Davies: 5 as *Vellica longipennis*

2001 Herman: 376 as *Vellica longipennis*

2001 Newton *et al*.: 341 as *Vellica longipennis*

Habitus. (Fig. 1.4B) 2.7–3.6 mm long. Light brown to dark brown, legs and antennae sometimes lighter.

Head. Width across eyes to length of head slightly wider than long. Interantennal groove absent. Anteocellar foveae moderately large, deeply impressed. Eyes moderately pubescent on ventral half, with more than 10 setae (Fig. 1.36C). Antennae with segments 3–10 each 1.3–1.9 times longer than wide, segments 4–11 each with many sensory pits with groups of pore-like openings. Ocelli absent. Nuchal constriction vague. Mandibles with molar area

with L-shaped row of setae (Fig. 1.32C). Labrum with sensory pores along anterior margin only. Labial palpi with third segment 1.4–1.8 times longer than segment 2.

Thorax. Pronotum narrow (Fig. 1.15G), length to width ratio = 0.79–0.87; ratio of width of pronotum to width of head = 1.11–1.33; maximum width slightly narrower than elytra at base; punctures separated by average distance subequal to or slightly greater than diameter of one puncture; lateral margins very narrowly explanate just posterad the lateral fovea, otherwise not at all explanate anterad or posterad the lateral foveae. Foveae broad, moderately deeply impressed, narrowly separated from lateral margins. Elytra with humeral angles convex; epipleural carina not projecting; 2.2–2.4 times longer than pronotum; apical margins convex. Wings developed or brachypterous. Mesosternum with projecting tooth; longitudinal carina along midline of mesosternum present, becoming vague near posterior margin (Fig. 1.20A).

Abdomen. Tergites IV and V each with wing folding spicules very broad, nearly contiguous or contiguous in shape of single transverse band. Apical palisade fringe on tergite VII absent.

Legs. Pro-, meso-, and metatibia evenly pubescent to apex. Metatrochanter without tooth on apical margin.

Aedeagus. (Fig. 1.21C) 0.68–0.78 mm long. Median lobe narrowly triangular. Parameres narrow; diverging near base then parallel. Internal sac small, narrowly elongate; with patch of large microspinules.

Type specimens. Lectotype, male, with labels as follows: Oct./Placer Co., CAL./TYPE USNM 48113/Vellica longipennis Cas./LECTOTYPE ♂ Vellica longipennis Csy., desig. 1984, J.M. Campbell. The Casey collection also contains six paralectotypes, all labeled "Siskiyou Co., Cal." All specimens are deposited in the USNM, Washington, DC.

Distribution. (Fig. 1.12B) *Phlaeopterus longipennis* is known from northern California in the Sierras, Cascades, and Trinity Mountains, through Oregon to Mt. Rainier National Park, Washington. Adults have been collected at 500–3000 m elevation from May–August in wet moss at the edges of cold streams.

Remarks. *Phlaeopterus longipennis* can be differentiated from all other *Phlaeopterus* species but *P. obsoletus* by its absence of ocelli. *Phlaeopterus longipennis* is externally similar to *P. obsoletus*, but differs significantly in aedeagal characters, and can be externally differentiated by the punctation of the head and pronotum, its slightly shorter elytra, and by its smaller overall size. *Phlaeopterus longipennis* matches the diagnosis of the genus *Phlaeopterus* given herein and so is moved from the monotypic genus *Vellica*, Casey, 1885, making *Vellica* a synonym under *Phlaeopterus*. This transfer was also suggested by Newton *et al.* (2000).

1.5.4.15 *Phlaeopterus obsoletus* Campbell n. sp.

Figs. 1.4C, 1.13A, 1.15H, 1.17G, 1.20B, 1.21D, 1.29A, 1.31G, 1.32I–1.32J, 1.33G, 1.34E–1.34F, 1.37E, 1.39C–1.39D, 1.40A

Type locality: Berkeley Park, Mt. Rainer National Park, Washington, USA

1957 Hatch: 461 [misidentification] as *Vellica longipennis*

Habitus. (Fig. 1.4C) 2.9–3.9 mm in length. Light brown to dark brown, legs lighter, antennae sometimes lighter.

Head. Width across eyes to length of head slightly wider than long (Fig. 1.34E–1.34F). Interantennal groove absent. Anteocellar foveae moderately large, deeply impressed. Eyes moderately pubescent on ventral half, with more than 10 setae. Antennae with segments 3–10 each 1.3–1.9 times longer than wide, segments 4–11 each with many sensory pits with groups of pore-like openings (Fig. 1.37E). Ocelli absent. Nuchal constriction vague. Mandibles with molar area with L-shaped row of setae. Epipharynx (Fig. 1.33G). Maxillary palpus (Figs. 1.32I–1.32J, 1.39C–1.39D). Labrum with sensory pores along anterior margin only (Fig. 1.31G). Labial palpi with third segment 1.4–1.8 times longer than segment 2.

Thorax. Pronotum narrow (Fig. 1.15H), length to width ratio = 0.79–0.88; ratio of width of pronotum to width of head = 1.25–1.33; maximum width slightly narrower than elytra at

base; punctures separated by average distance subequal to or slightly greater than diameter of one puncture; lateral margins not explanate anterad or posterad the lateral fovea; lateral foveae moderately deeply impressed, narrowly separated from lateral margins. Elytra with humeral angles convex; epipleural carina not projecting; 2.0–2.3 times longer than pronotum; apical margins convex. Wings developed or brachypterous. Mesosternum with projecting tooth; longitudinal carina along midline of mesosternum vaguely present, becoming obscured on posterior half (Fig. 1.20B).

Legs. Pro-, meso-, and metatibia evenly pubescent to apex. Metatrochanter without tooth on apical margin.

Abdomen. Tergites IV and V each with wing folding spicules very broad, nearly contiguous or contiguous in shape of single transverse band. Apical palisade fringe on tergite VII absent.

Aedeagus. (Fig. 1.21D) 0.52–0.63 mm long. Median lobe short, oblong, sides subparallel, apex broadly convex. Parameres diverging in basal half. Internal sac large; with two mediolateral patches of microspinules.

Type specimens. Holotype, male (UAMObs:Ento:235217), and allotype, female (UAMObs:Ento:235837), each with labels as follows: WASH, Mt. Rainer N.P., Berkeley Park, 3.5 mi. W. Sunrise, 6700', 8.VIII.1975, J.M. & B.A. Campbell/ HOLOTYPE ♂ (or ALLOTYPE ♀)

Phlaeopterus obsoletus desig. 1984, J.M. Campbell, CNC No. 18470. Both specimens are deposited in the CNC, Ottawa.

Paratypes: 878, deposited in the AMNH, BMNH, CAS, CSCA, CNC, FMNH, MCZ, OSAC, USNM.

Distribution. (Fig. 1.13A) *Phlaeopterus obsoletus* is known from the Cascade Range in British Columbia, Oregon, and Washington, and from Jasper National Park, Alberta. Adults have been collected at 1000–2130 m elevation from May–August in wet moss at the edges of streams or in the splash zone of waterfalls.

Remarks. *Phlaeopterus obsoletus* can be distinguished from all other *Phlaeopterus* species but *P. longipennis* by the absence of ocelli. *Phlaeopterus obsoletus* and *P. longipennis* are very similar but can be differentiated by characters discussed in the remarks section of the latter species. This species has been misidentified as *P. longipennis* in most collections as well as by Hatch (1957).

Etymology. This species name is derived from the Latin adjective for effaced or indistinct, referring to the absence of ocelli.

1.5.4.16 *Phlaeopterus occidentalis* Campbell n. sp.

Figs. 1.4D, 1.13B, 1.16F, 1.20E, 1.23D, 1.24A

Type locality: Mt. Rainier National Park, Washington, USA

1893 Casey: 402 [misidentification] as *Tilea cavicollis*

Habitus. (Fig. 1.4D) 6.1–8.2 mm in length. Reddish-brown to black; elytra sometimes lighter than pronotum; palpi, legs, and antennae reddish-brown to black.

Head. Width across eyes to length of head subequal to slightly wider than long. Interantennal groove broadly and moderately deeply impressed. Anteocellar foveae large, deeply impressed. Eye pubescence absent, or with less than 10 scattered setae near ventral margin. Antennae with segments 5–10 at least 2 times longer than wide; segments 4–11 each with many sensory pits with papilliform projections. Ocelli present. Nuchal constriction vague. Mandibles with molar area with L-shaped row of setae. Labrum with sensory pores along entire surface. Labial palpi with third segment 1.6–1.8 times longer than segment 2.

Thorax. Pronotum moderately wide (Fig. 1.16F), length to width ratio = 0.63–0.71; ratio of width of pronotum to width of head = 1.45–1.70; maximum width subequal to elytra width at humeral angle; punctures on dorsal surface separated by distance slightly less than to slightly more than diameter of one puncture; lateral margins explanate posterad the lateral foveae, narrowly explanate anterad the lateral foveae, narrowing to not at all explanate at apex; lateral foveae deeply impressed. Elytra with humeral angles convex; epipleural carina not projecting; 2.2–2.6 times longer than pronotum; apical

margins broadly convex. Wings nearly always fully developed, rarely brachypterous. Mesosternum with projecting tooth; longitudinal carina along entire midline of mesosternum (Fig. 1.20E).

Legs. Apex of pro-, meso-, and metatibia without pubescence, subglabrous apex of metatibia length as ratio to metatibia length in males = 7.6–28.0, in females = 8.6–19.4. Metatrochanter without tooth on apical margin.

Abdomen. Wing-folding spicules on tergites IV and V broad, transverse, narrowly separated; tergite VI with wing-folding spicules.

Aedeagus. (Figs. 1.23D, 1.24A) 1.24–1.50 mm long. Median lobe irregularly narrowing from base to apex, apex abruptly truncate. Parameres diverging from base to apical fourth, apical fourth strongly converging towards apex of median lobe. Internal sack lightly sclerotized; with subapical transverse fold; apical two-thirds covered in microspinules except for smooth area of transverse fold.

Primary types. Holotype male (UAMObs:Ento:235826), and allotype female (UAMObs:Ento:235827), each with labels as follows: WASH., Mt. Rainier N. P., end of West Side Rd., 3.VIII.1979, 3700', J. M. & B. A. Campbell/HOLOTYPE ♂ (or ALLOTYPE ♀) Phlaeopterus occidentalis desig. 1984, J. M. Campbell CNC No. 18466. Both specimens are in the CNC, Ottawa. Paratypes: 232 deposited in the AMNH, CAS, CSCA, CNC, FMNH, MCZ, ROM, USNM, UCRC.

Distribution. (Fig. 1.13B) *Phlaeopterus occidentalis* is known from southern California north through Oregon, Washington, and British Columbia to Southeast Alaska. A single specimen (UAM:Ento:332755) was collected from Great Basin National Park, Nevada. Adults of this species have been collected from 300–3200 m, a broader elevation range than any other species in the genus, but have only been collected from 300–1800 m in British Columbia and Alaska. Adults have been collected from May–October in California and Oregon, but only June–August in Washington and Alaska. This species has been collected under rocks and in moss in the splash-zone at the edges of small streams or waterfalls. We attempted to re-collect this species from the 1968 locality (UAMObs:Ento:233463) near Haines, Alaska, in the summer of 2014 but were unsuccessful.

Remarks. Specimens from Vancouver Island vary from those of the mainland by having the base of the internal sac of the aedeagus broader, and by having the apex of the internal sac concave. The aedeagus of the Vancouver Island (Fig. 1.24A) and mainland (Fig. 1.23D) populations are illustrated. There is also a slight difference in the length of the posterior tibiae vs. posterior tarsus and in the length of the antennal segments approaching the apex. Furthermore, the mainland population shows geographic variation in the aedeagus, with the aedeagus becoming slightly longer and the apex of the median lobe progressively more narrowly triangular moving from south to north. We have deemed these differences insufficient to warrant splitting these populations into multiple species or subspecies.

Casey (1893) erroneously referred to a specimen of *P. occidentalis* as *P. cavicollis* Fauvel in his treatment of the latter species, likely because the type series of the latter species was

mixed. This error was fixed by a lectotype designation for *P. cavicollis.* The specimen examined by Casey (1893) is labeled as follows: Vanc./♀/CASEY bequest 1925/cavicollis Fvl./May be from original type series. – see Casey, Col. notices V. 1893, p. 402.

Etymology. This species is named for its wide distribution in northwestern North America.

1.5.4.17 *Phlaeopterus olympicus* Campbell n. sp.

Figs. 1.5A, 1.14A, 1.16G, 1.20C, 1.24B, 1.36F

Type locality: Olympic National Park, Washington, USA

Habitus. (Fig. 1.5A) 6.3–8.2 mm in length. Dark-brown to reddish-brown; legs, elytral epipleurae, and palpi brown to reddish-brown; elytra often lighter than pronotum.

Head. Width across eyes to length of head subequal to slightly wider than long. Interantennal groove broadly and shallowly impressed. Anteocellar foveae large, deeply impressed. Eye pubescence absent or with less than 10 setae near ventral margin (Fig. 1.36F). Antennae with segments 5–10 at least 2 times longer than wide; segments 4–11 each with many sensory pits with papilliform projections. Ocelli present. Nuchal constriction vague. Mandibles with molar area with L-shaped row of setae. Labrum with

sensory pores along entire surface. Labial palpi with third segment 1.6–1.8 times longer than segment 2.

Thorax. Pronotum moderately wide (Fig. 1.16G), length to width ratio = 0.68–0.72; ratio of width of pronotum to width of head = 1.52–1.59; maximum width subequal to elytra width at humeral angle; punctures on dorsal surface separated by distance equal to diameter of one puncture; lateral margins explanate posterad but not anterad the lateral foveae; lateral foveae deeply impressed. Elytra with humeral angles convex; epipleural carina not projecting; 2.2–2.5 times longer than pronotum; apical margins broadly convex. Wings nearly always fully developed, rarely brachypterous. Mesosternum with projecting tooth; longitudinal carina along midline of mesosternum indistinct (Fig. 1.20C).

Legs. Apex of pro-, meso-, and metatibia without pubescence, subglabrous apex of metatibia length as ratio to metatibia length = 8.3–20.0. Metatrochanter without tooth on apical margin.

Abdomen. Wing-folding spicules on tergites IV and V broad, transverse, narrowly separated; tergite VI lacking wing-folding spicules.

Aedeagus. (Fig. 1.24B) 1.50–1.60 mm long. Median lobe broadly triangular, margins narrowing more sharply nearing apex. Parameres not or barely curved towards apex of median lobe, originating near middle of median lobe. Internal sac broadly triangular, lightly sclerotized, covered with microspinules.

Type specimens. Holotype male (UAMObs:Ento:235824), and allotype female (UAMObs:Ento:235825), each with labels as follows: WASH. Olympic N.P., 0.5 mi S Lake No. 8 (7 Lakes Basin) 5000', 16.VIII.1979, J.M. and B.A. Campbell/HOLOTYPE ♂ (or ALLOTYPE ♀) Phlaeopterus olympicus, desig. 1984, J.M. Campbell, CNC No. 18464. Both specimens are in the CNC, Ottawa. Paratypes: 305 deposited in the AMNH, CAS, CSCA, CNC, FMNH, MCZ, USNM.

Distribution. (Fig. 1.14A) *Phlaeopterus olympicus* is known only from the Olympic Mountains of Washington State, inside Olympic National Park and from a single specimen (UAMObs:Ento:234159) from Harts Pass, Okanagan County, Washington. Adults of this species have been collected from July–August at 650–1970 m elevation, with most specimens collected between 1500–1800 m elevation. Adults have been collected while feeding on arthropods on the surface of snowfields at night and during the day under wet rocks and gravel at the edges of snowfields or in moss or wet rocks at the edges of cold streams flowing from snowfields. Some specimens have been collected at lower elevations under stones or in moss along the edges of the Soleduck River or in moss and under stones at the edges of streams draining high-elevation lakes.

Remarks. *Phlaeopterus olympicus* can be distinguished from all other *Phlaeopterus* species by the lack of a mesosternal carina but presence of a mesosternal tooth, its pronotal shape, and its glabrous apex of the tibiae. *Phlaeopterus olympicus* is most similar to *P. loganensis*, from which it may be distinguished by having the apex of the elytra broadly convex, and by

the shape of aedeagus. *Phlaeopterus olympicus* and *P. loganensis* are the only two species of the genus completely lacking a carina along the midline of the mesosternum, although the carina is vague, especially on the posterior half, in other species. *P. olympicus* has not been collected since 1984, despite three other species having been collected recently from the Olympic Mountains: *P. fusconiger* as recently as 2014 (UAM:Ento:299528), *P. cavicollis* as recently as 2008 (UAMObs:Ento:232734), and *P. lagrandeuri* as recently as 1996 (UAMObs:Ento:234415).

Etymology. The specific epithet *olympicus* is derived from the type locality.

1.5.4.18 *Phlaeopterus smetanai* Campbell n. sp.

Figs. 1.5B, 1.14B, 1.16E, 1.23B–1.23C, 1.33H

Type locality: Mt. Hood National Forest, Oregon, USA

Habitus. (Fig. 1.5B) 6.0–9.0 mm in length. Black; usually darker than any other *Phlaeopterus* species; legs, palpi, and antennae sometimes lighter, dark brown.

Head. Head broad, ratio of width across eyes to length of head about 5:4. Interantennal groove broadly and deeply impressed. Anteocellar foveae large, deeply impressed. Eye pubescence absent, or with less than 10 scattered setae near ventral margin. Antennae with

segments 5–10 at least 2 times longer than wide; segments 4–11 each with many sensory pits with papilliform projections. Ocelli present. Nuchal constriction vague. Epipharynx (Fig. 1.33H). Mandibles with molar area with L-shaped row of setae. Labrum with sensory pores along entire surface. Labial palpi with third segment 1.6–1.8 times longer than segment 2.

Thorax. Pronotum somewhat broad (Fig. 1.16E), length to width ratio = 0.63–0.77; ratio of width of pronotum to width of head = 1.49–1.67; maximum width subequal to elytra width at humeral angle; punctures on dorsal surface separated by average distance slightly greater than diameter of one puncture; lateral margins explanate posterad the lateral foveae, progressively more narrowly explanate from lateral foveae to just before apex; lateral foveae deeply impressed. Elytra with humeral angles convex; epipleural carina not projecting; 2.3–2.6 times longer than pronotum; apical margins broadly convex. Wings nearly always fully developed, rarely brachypterous. Mesosternum with projecting tooth, tooth more strongly notched on posterior margin than on anterior margin; longitudinal carina along midline of mesosternum complete.

Legs. Pro-, meso-, and metatibia with dense pubescence to apex or with small glabrous region at apex, if with glabrous region, length of glabrous apex of mesotibia shorter than length of basal mesotarsomere. Metatrochanter without tooth on apical margin.

Abdomen. Wing-folding spicules on tergites IV and V broad, transverse, narrowly separated; tergite VI lacking wing-folding patches.

Aedeagus. (Figs. 1.23B–1.23C) 1.28–1.67 mm long. Median lobe roughly triangular, evenly to convexly narrowed from base to apex. Parameres slightly diverging from base to near apex then converging; ending just beyond to distinctly beyond apex of median lobe. Internal sac elongate, roughly rectangular, narrowed from base to apex; apex subtruncate; lightly sclerotized; more densely covered in microspinules on apical half.

Type specimens. Lectotype male (UAMObs:Ento:235828), and paralectotype female (UAMObs:Ento:235829), with label data as follows: ORE., Mt. Hood N. F., Tilly Jane Cr., 7000' 31.VII.1979, J. M. & B. A. Campbell/ LECTOTYPE ♂ (or ALLOTYPE ♀) Phlaeopterus smetanai, desig. 1984, J. M. Campbell CNC No. 18465. Both specimens are in the CNC, Ottawa. Paratypes: 504, deposited in AMNH, NHMUK, CAS, CSCA, CNC, FMNH, MCZ, OSAC, ROM, USNM, UCRC, and RBC.

Distribution. (Fig. 1.14B) *Phlaeopterus smetanai* is broadly distributed in the northwestern United States from Washington east to Idaho and south to Colorado, Arizona, and southern California. Adults have been collected from April–October at elevations of 360–3000 m. Adults have been collected under rocks and in moss from the edges of cold streams or in the splash zones of waterfalls, as well as in gravel at the edges of springs and in one case from under rocks near a spring that had recently stopped flowing.

Remarks. *Phlaeopterus smetanai* is more uniformly black than any other *Phlaeopterus* species. It is most similar to *P. occidentalis*, from which it can be distinguished by its darker color, having the glabrous region at the apex of the mesotibia shorter, and by aedeagal

characters, including lacking the subapical transverse fold of the latter species. A population near Payson, Arizona differs from other specimens by the shape and larger size (1.60–1.67 mm vs. 1.28–1.52 mm) of the aedeagus (Payson population aedeagus in Fig. 1.23C, main population aedeagus in Fig. 1.23B). Genetic analysis could help determine if this population is a distinct species, but all attempts to sequence DNA from *P. smetanai* specimens in Chapter 2 were unsuccessful.

Etymology. This species was named in honor of Dr. Ales Smetana, Biosystematics Research Institute, Ottawa, Canada.

1.6 Discussion

This taxonomic revision of *Phlaeopterus* is based in significant part on the unpublished work on the genus by J.M. Campbell from the 1980's. We have agreed with Campbell's (unpublished) conclusions in most cases, but differ most significantly in the cases of subgenera, species groups, and some subspecies. We do not recognize any subgenera or species groups in the genus *Phlaeopterus*. These intrageneric ranks are most useful to subdivide large chunks of diversity to make identification keys more useful, and as a proxy for phylogenetic relationships. Neither is applicable here because *Phlaeopterus* is not a particularly large genus and we now have a more quantitative estimate of the phylogeny of the genus (Chapter 2).

Similarly, we have not recognized the subspecies proposed in Campbell (unpublished), except in the case of *P. castaneus castaneus* and *P. castaneus cascadiensis*.

Although other potential subspecies have similar morphological diversity (see remarks sections of *P. occidentalis* and *P. cavicollis*) subspecies status is justified in this case by the phylogenetic analysis of mitochondrial COI data of Chapter 2, which recovered the two subspecies as well-supported reciprocally monophyletic clades. The designation of these two subspecies acknowledges the high morphological similarity of these populations while simultaneously recognizing two distinct genetic lineages. The two subspecies are morphologically diagnosable throughout their range, but intermediate forms can be found in Garibaldi and Manning Provincial Parks, Canada. The greater than 4% pairwise difference in COI sequence data between these two subspecies may be explained by hybridization between *P. castaneus castaneus* and *P. loganensis* (Chapter 2).

The unique snowfield and high-altitude stream habitat association of most *Phlaeopterus* species (Table 1.1) puts these beetles at significant risk of extirpation, or even extinction, by a warming climate. Two species, described here, P. *bakerensis* and *P. olympicus*, have not been collected since 1979 and 1984, respectively. These collection records may be evidence of climate-induced change in abundance or distribution of these species.

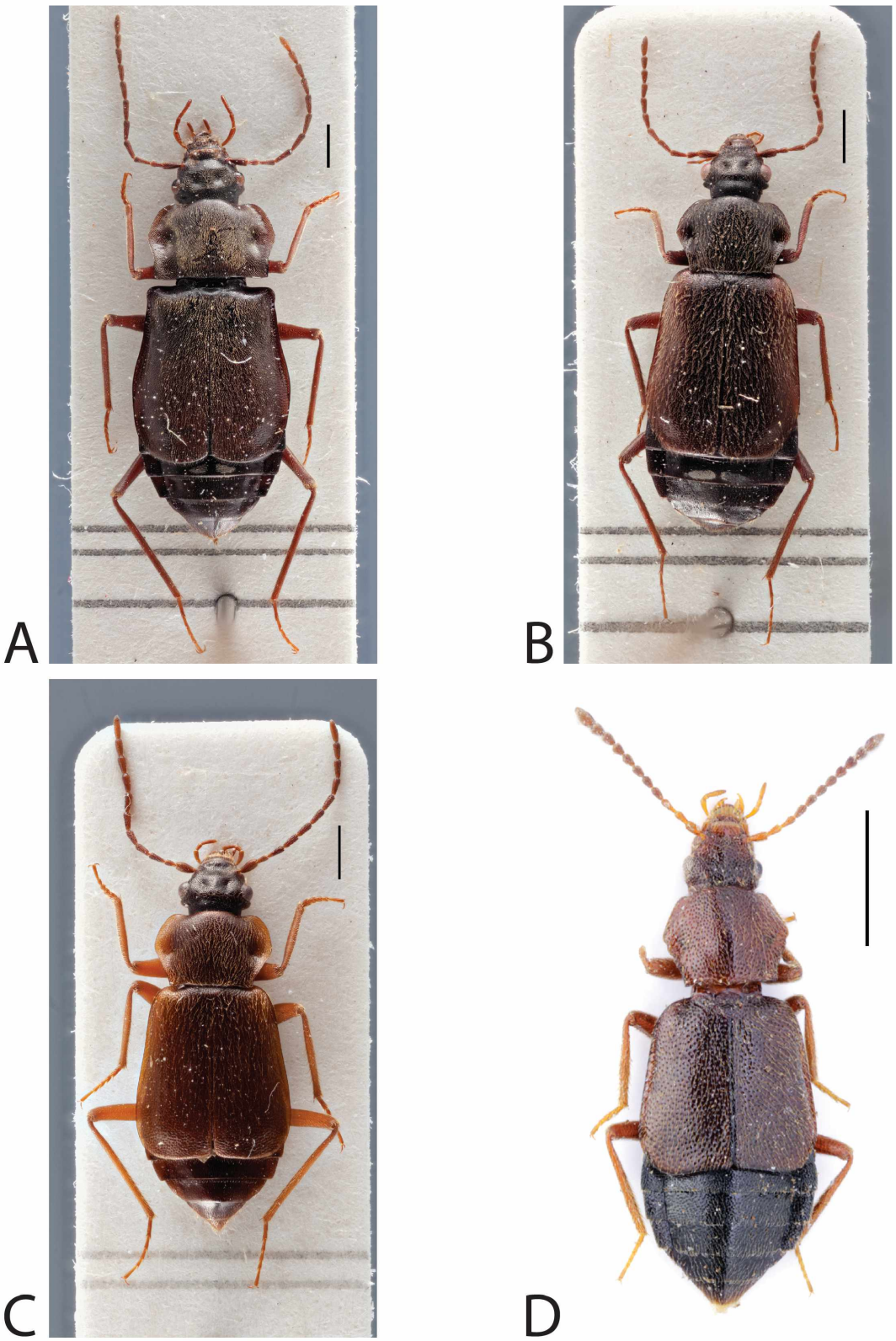

Figure 1.1. Habitus photographs of A) *Phlaeopterus bakerensis* female (UAMObs:Ento:233271), B) *P. castaneus* female (UAMObs:Ento:234040), C) *P. cavicollis* male (UAMObs:Ento:235795), and D) *P. czerskyi* female. Scale bars = 1 mm.

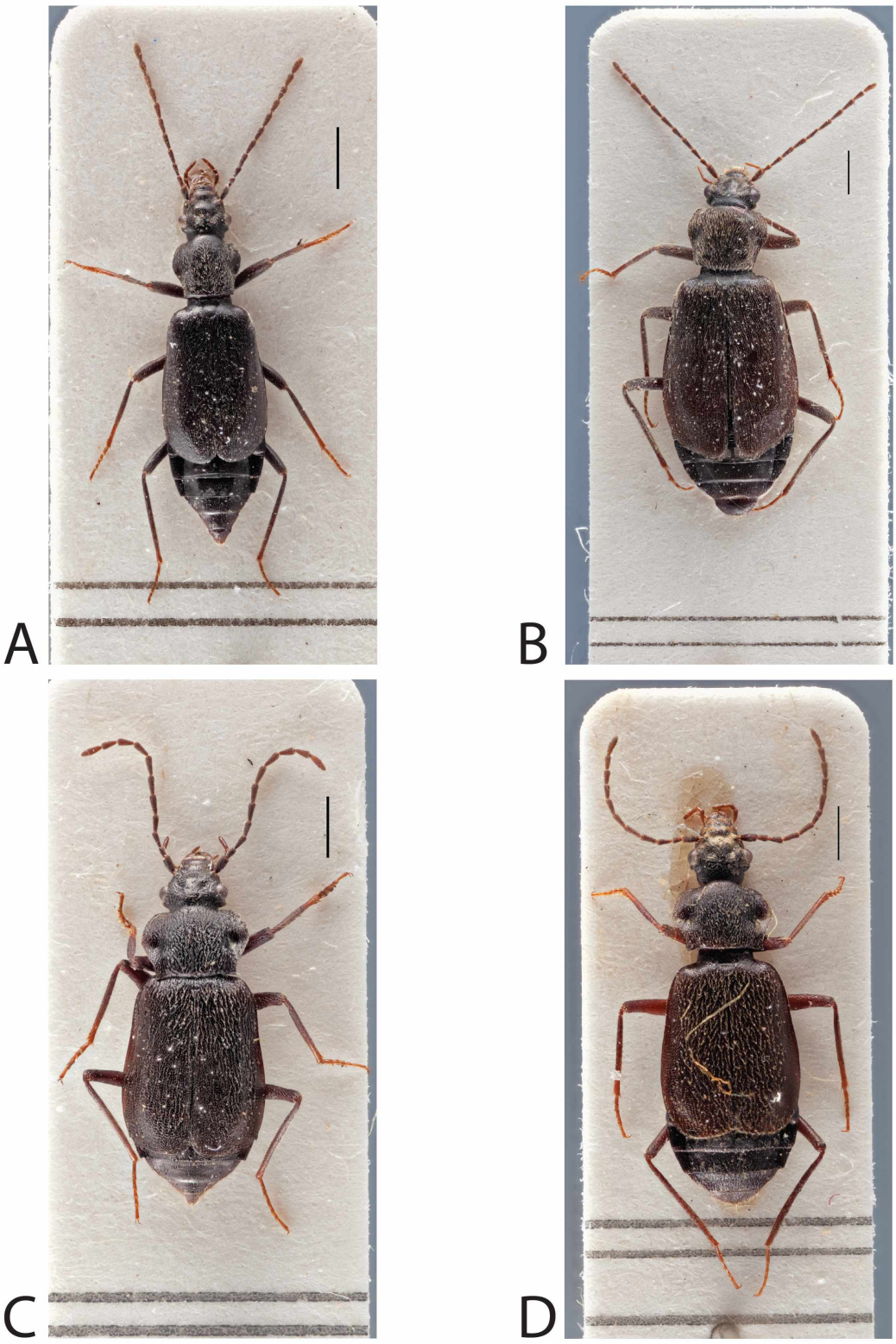

Figure 1.2. Habitus photographs of A) *Phlaeopterus elongatus* male (UAMObs:Ento:232543), B) *P. filicornis* female (UAM100366907), C) *P. frosti* male (UAMObs:Ento:235798), and D) *P. fusconiger* female (UAMObs:Ento:235496). Scale bars = 1 mm.

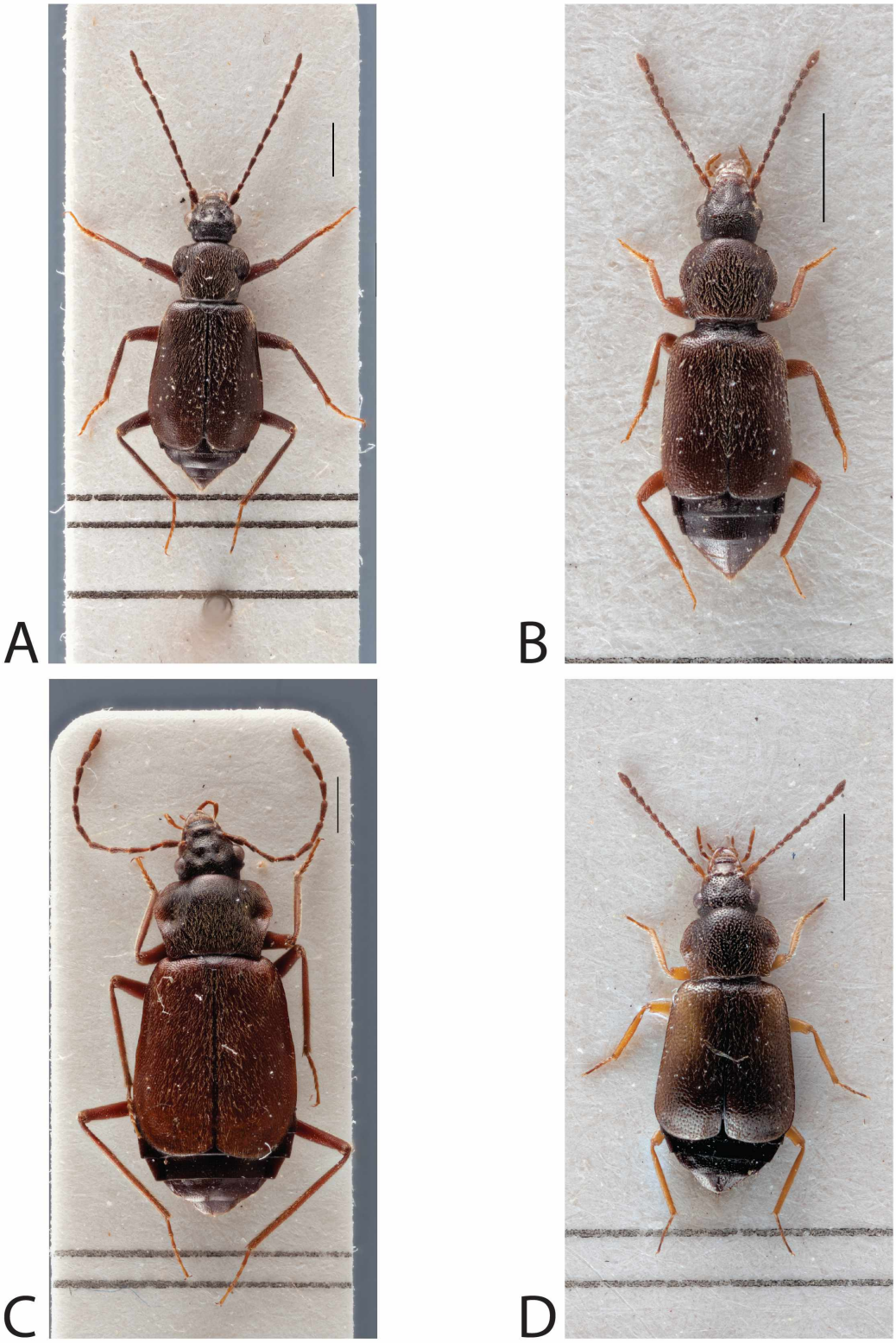

Figure 1.3. Habitus photographs of A) *Phlaeopterus hatchi* male (UAMObs:Ento:232429), B) *P. houkae* male (UAMObs:Ento:234115), C) *P. kavanaughi* female (UAMObs:Ento:232423), and D) *P. lagrandeuri* female (UAMObs:Ento:234056). Scale bars = 1 mm.

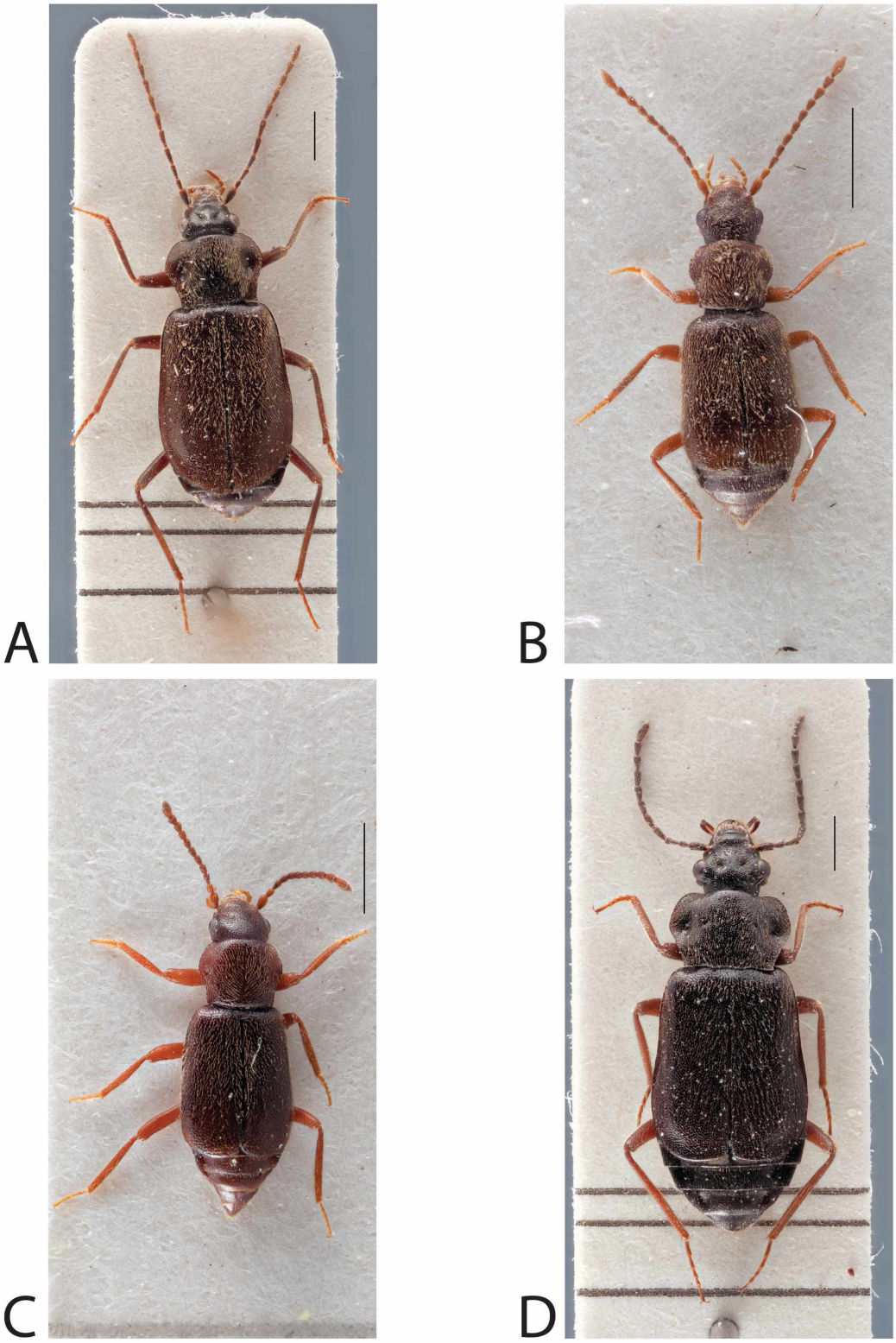

Figure 1.4. Habitus photographs of A) *Phlaeopterus loganensis* female (UAMObs:Ento:233072), B) *P. longipennis* male (UAMObs:Ento:235802), C) *P. obsoletus* male (UAMObs:Ento:233776), and D) *P. occidentalis* female (UAMObs:Ento:233445). Scale bars = 1 mm.

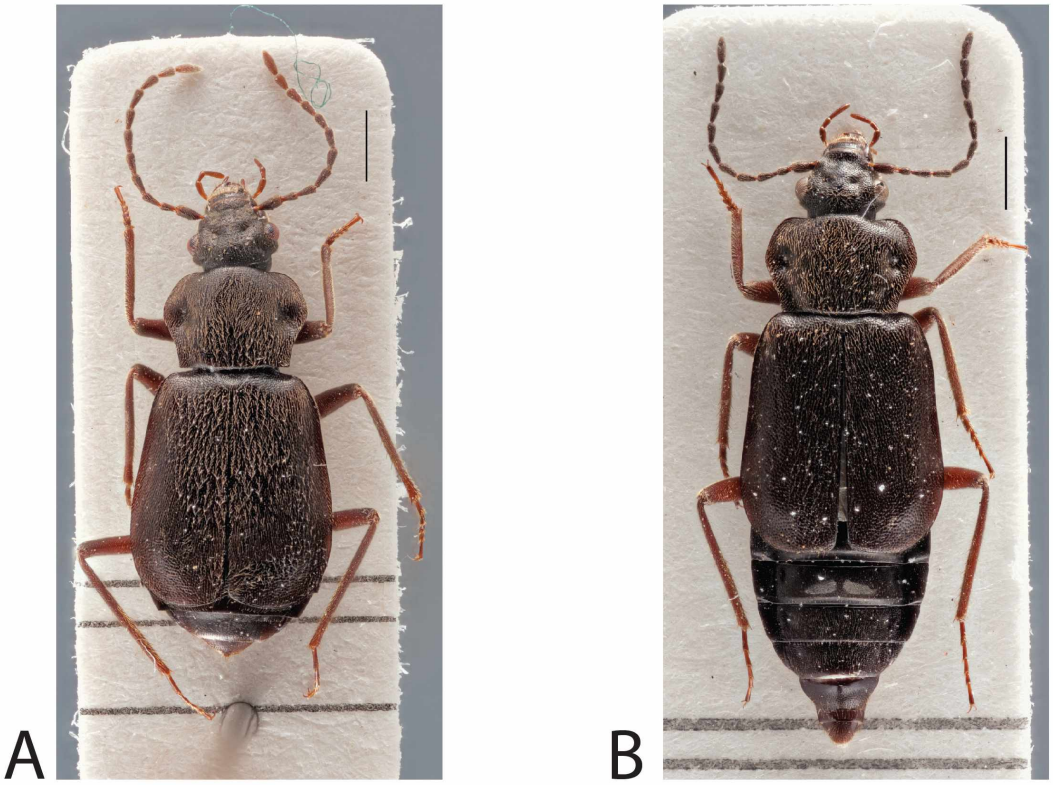

Figure 1.5. Habitus photographs of A) *Phlaeopterus olympicus* female (UAMObs:Ento:232960), and B) *P. smetanai* male (UAMObs:Ento:233301). Scale bars = 1 mm.

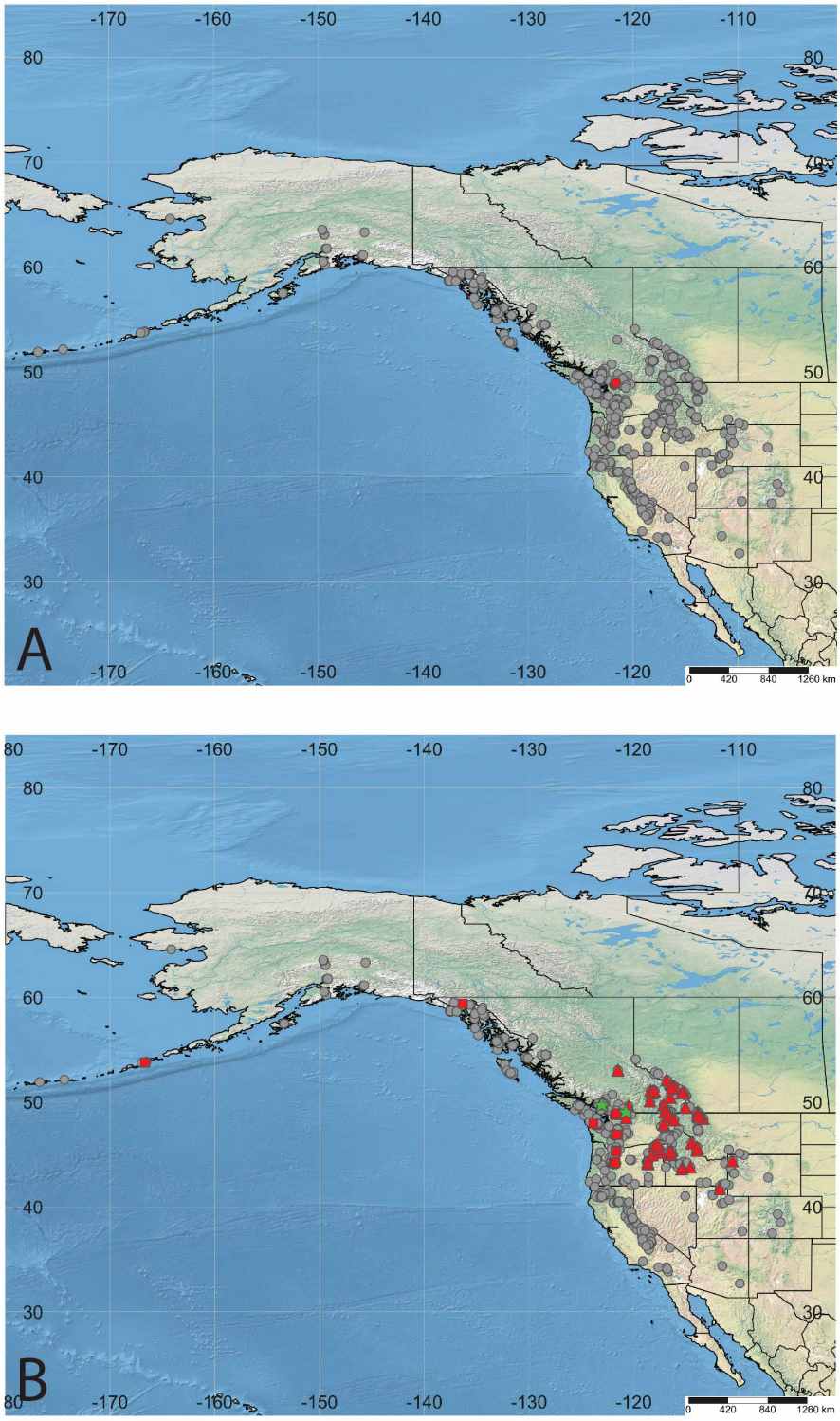

Figure 1.6. Distributions based on all specimen records georeferenced in this study of A) *Phlaeopterus bakerensis*, and B) *P. castaneus*. Grey dots represent localities where at least one *Phlaeopterus* species, but not the species of interest, was collected. Red dots represent localities where the species of interest was collected. In B), red triangles represent localities of *P. castaneus castaneus,* red squares represent localities of *P. castaneus cascadiensis*, and green stars represent areas of overlap of the two subspecies.

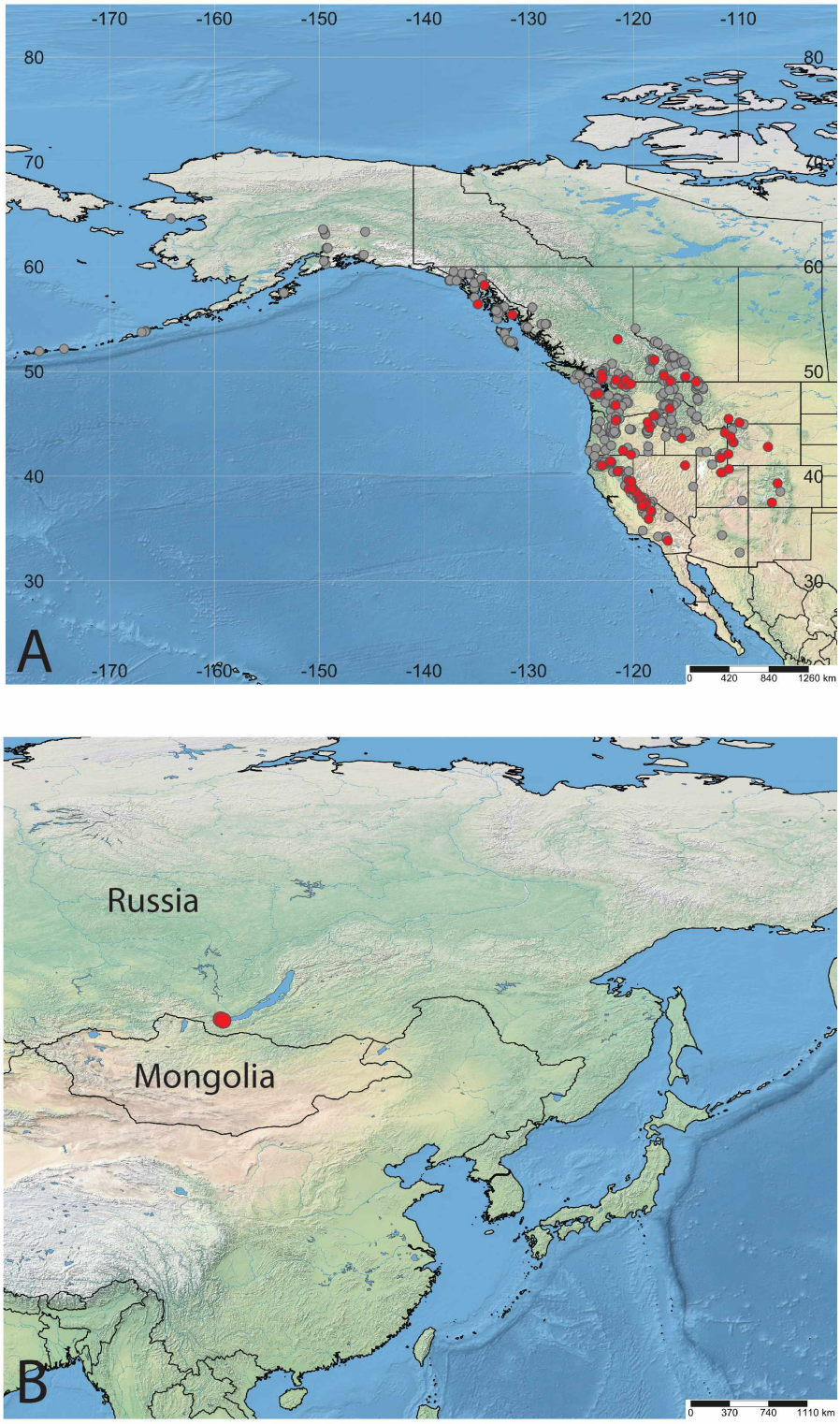

Figure 1.7. Distributions based on all specimen records georeferenced in this study of A) *Phlaeopterus cavicollis*, and B) *P. czerskyi*. Grey dots represent localities where at least one *Phlaeopterus* species, but not the species of interest, was collected. Red dots represent localities where the species of interest was collected.

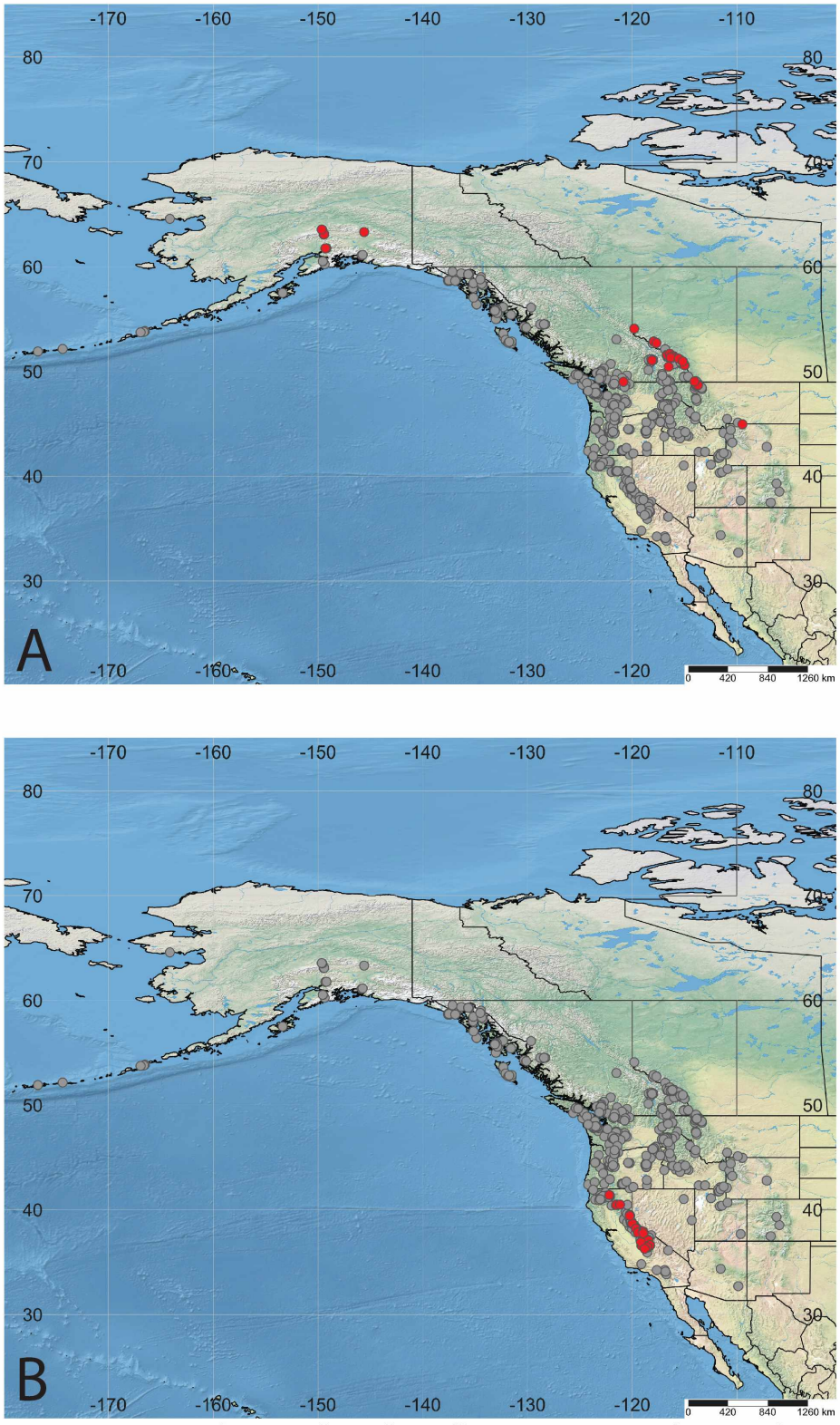

Figure 1.8. Distributions based on all specimen records georeferenced in this study of A) *Phlaeopterus elongatus*, and B) *P. filicornis*. Grey dots represent localities where at least one *Phlaeopterus* species, but not the species of interest, was collected. Red dots represent localities where the species of interest was collected.

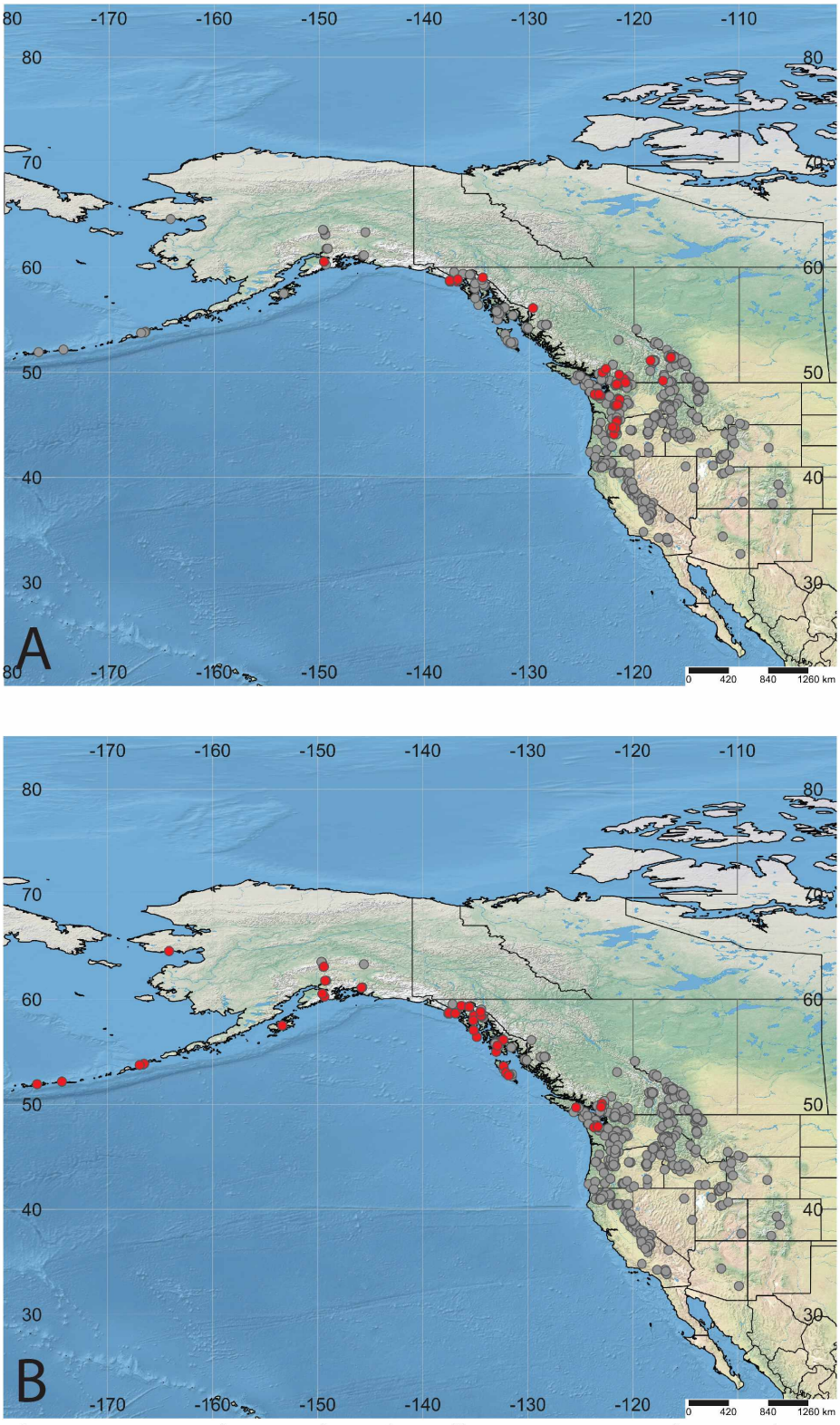

Figure 1.9. Distributions based on all specimen records georeferenced in this study of A) *Phlaeopterus frosti*, and B) *P. fusconiger*. Grey dots represent localities where at least one *Phlaeopterus* species, but not the species of interest, was collected. Red dots represent localities where the species of interest was collected.

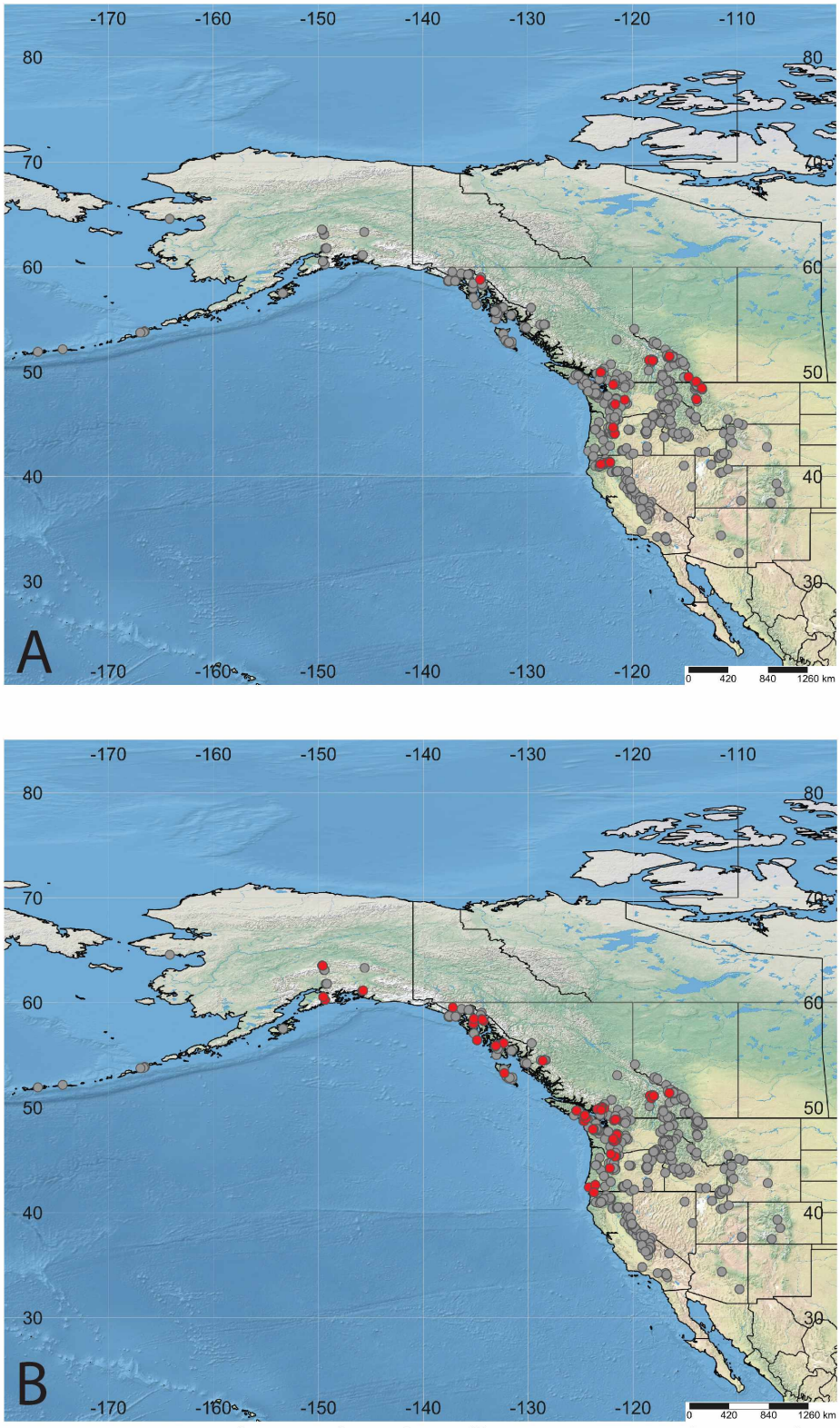

Figure 1.10. Distributions based on all specimen records georeferenced in this study of A) *Phlaeopterus hatchi*, and B) *P. houkae*. Grey dots represent localities where at least one *Phlaeopterus* species, but not the species of interest, was collected. Red dots represent localities where the species of interest was collected.

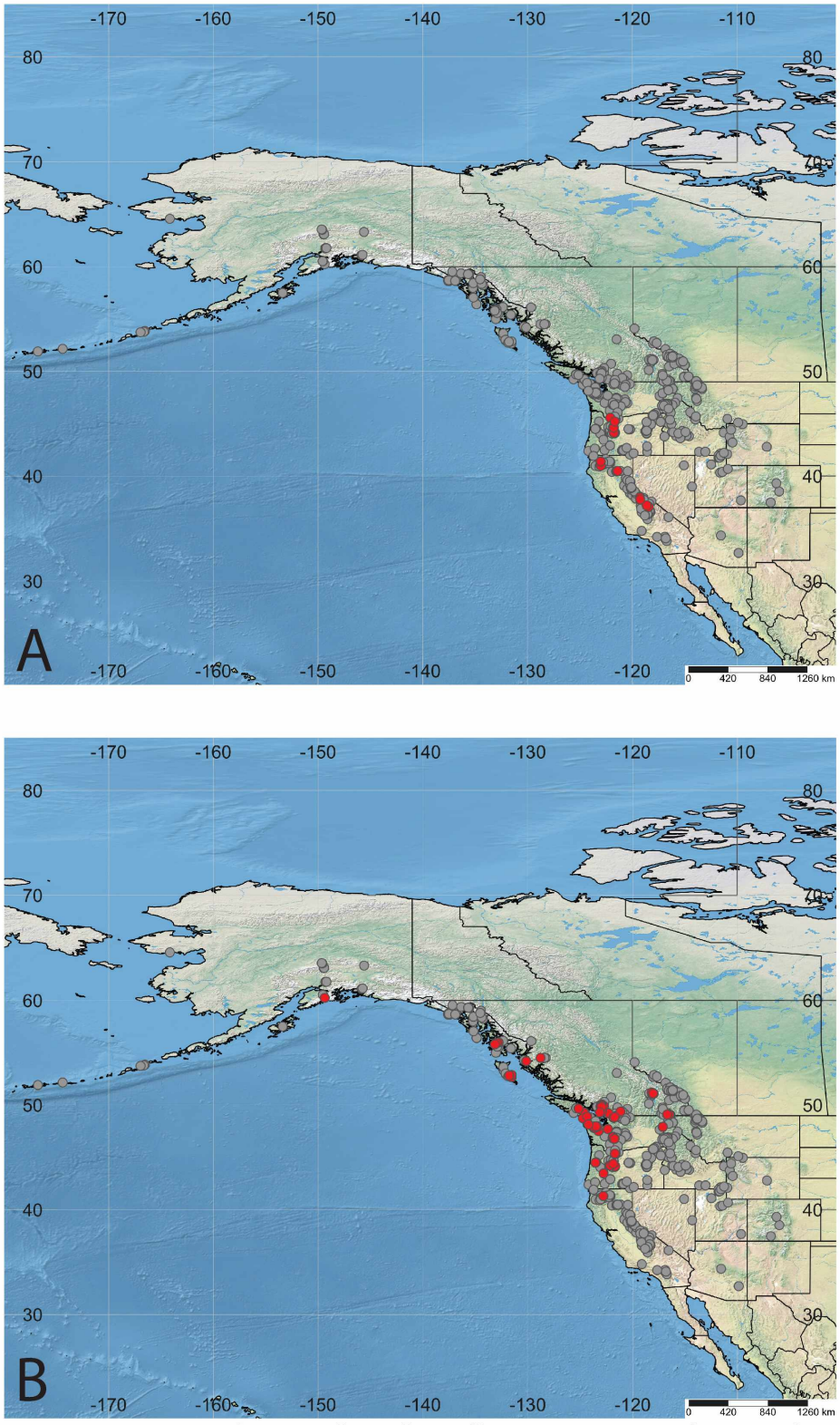

Figure 1.11. Distributions based on all specimen records georeferenced in this study of A) *Phlaeopterus kavanaughi*, and B) *P. lagrandeuri*. Grey dots represent localities where at least one *Phlaeopterus* species, but not the species of interest, was collected. Red dots represent localities where the species of interest was collected.

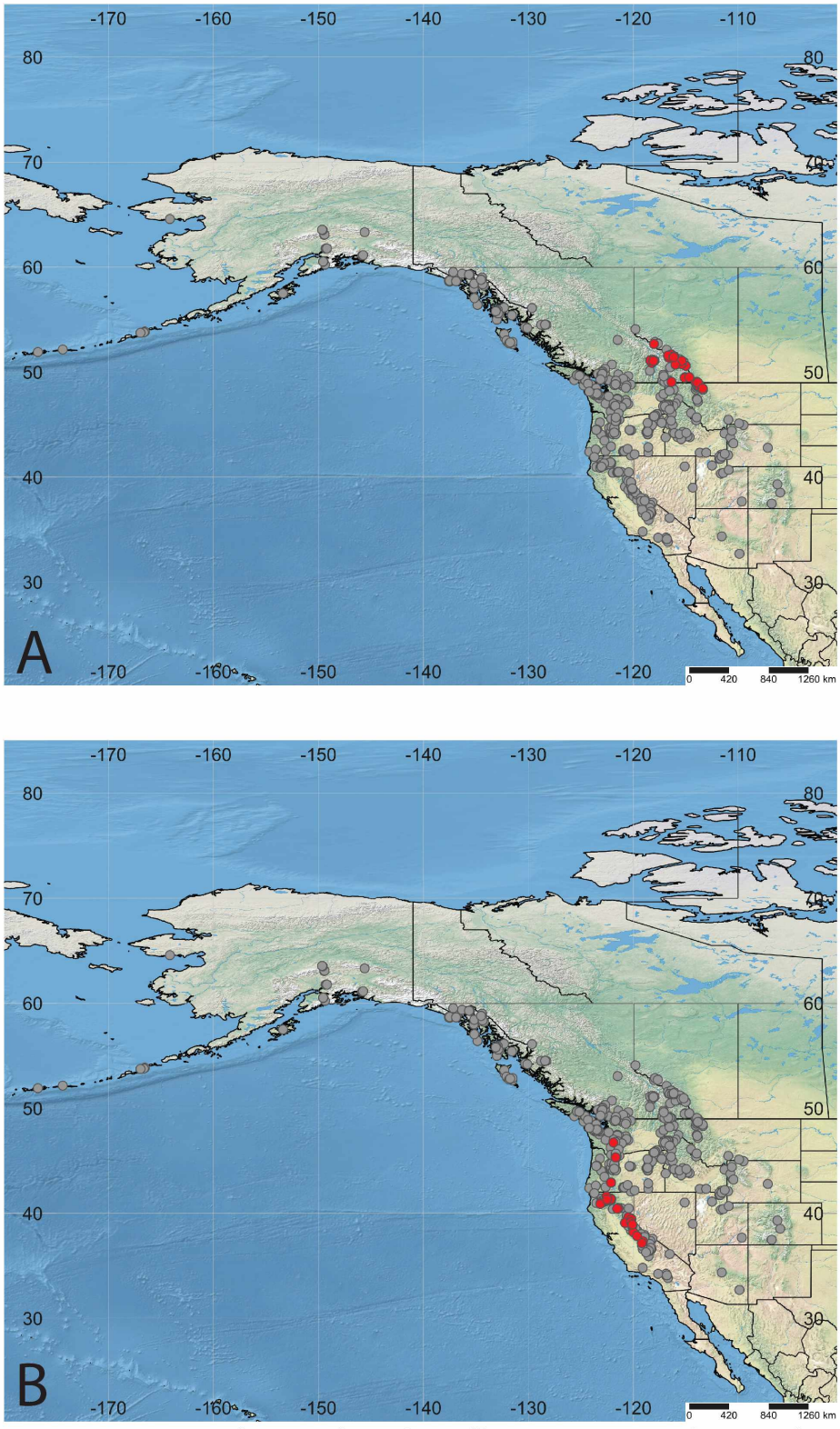

Figure 1.12. Distributions based on all specimen records georeferenced in this study of A) *Phlaeopterus loganensis*, and B) *P. longipennis.* Grey dots represent localities where at least one *Phlaeopterus* species, but not the species of interest, was collected. Red dots represent localities where the species of interest was collected.

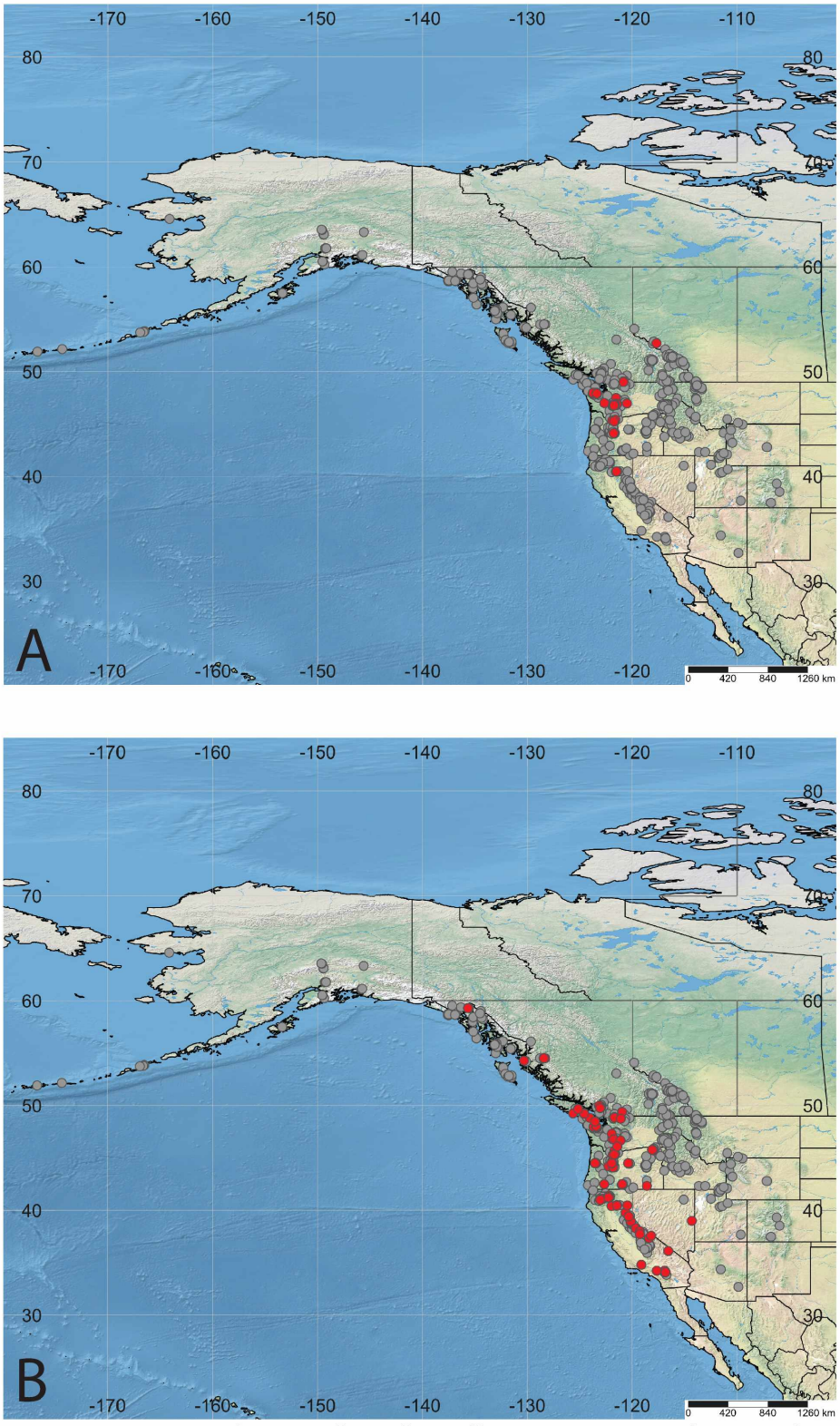

Figure 1.13. Distributions based on all specimen records georeferenced in this study of A) *Phlaeopterus obsoletus*, and B) *P. occidentalis.* Grey dots represent localities where at least one *Phlaeopterus* species, but not the species of interest, was collected. Red dots represent localities where the species of interest was collected.

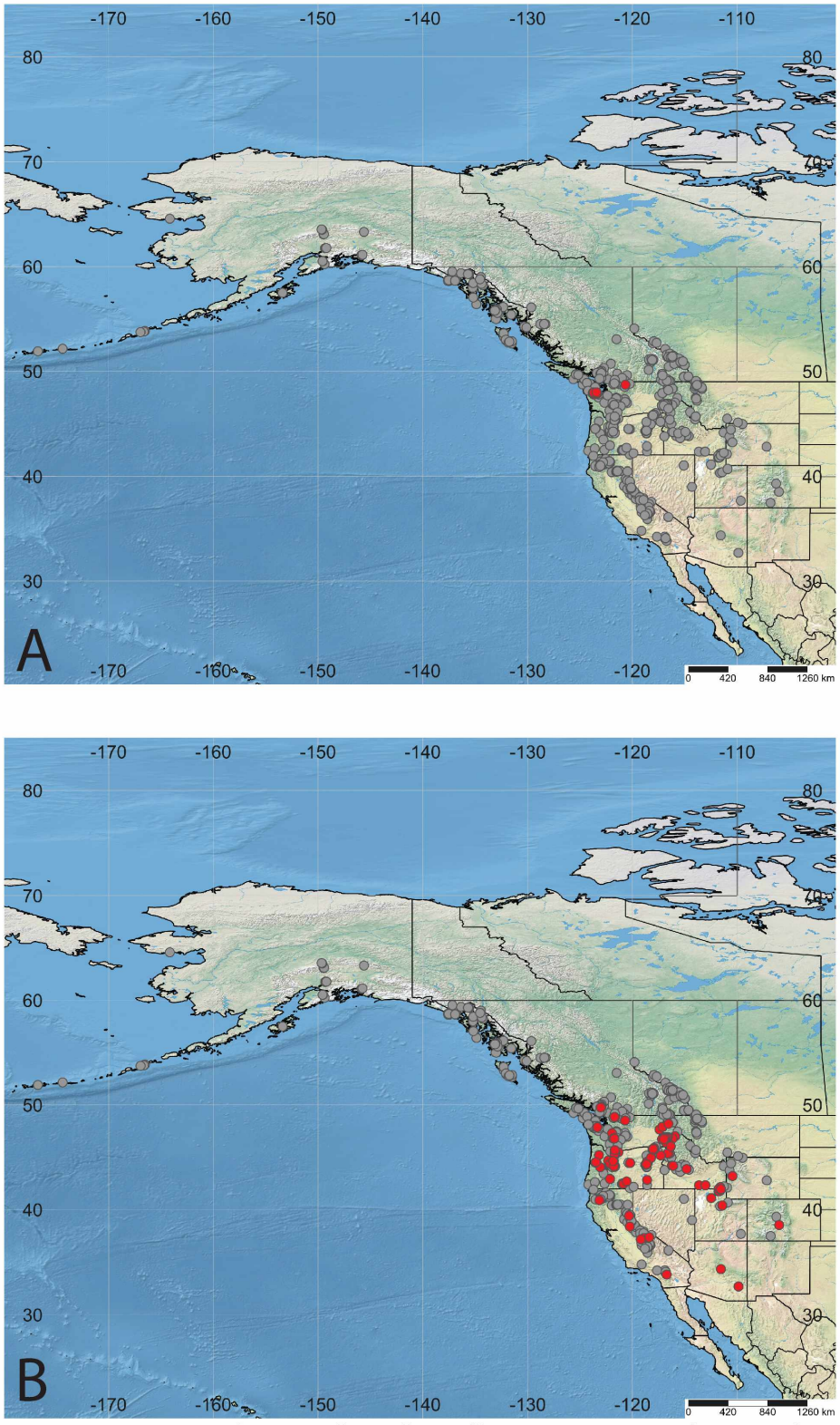

Figure 1.14. Distributions based on all specimen records georeferenced in this study of A) *Phlaeopterus olympicus*, and B) *P. smetanai.* Grey dots represent localities where at least one *Phlaeopterus* species, but not the species of interest, was collected. Red dots represent localities where the species of interest was collected.

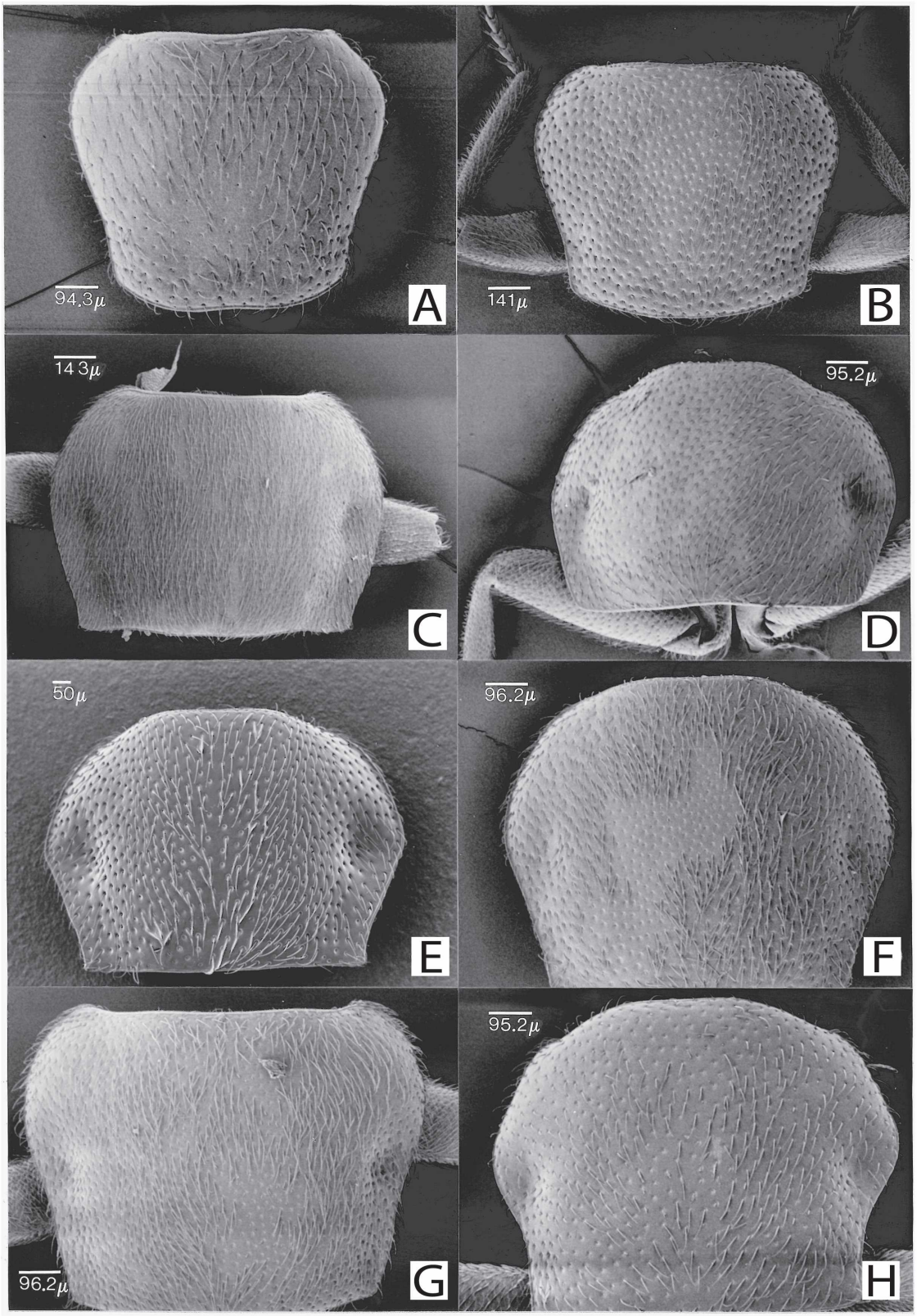

Figure 1.15. Dorsal view of pronotum of A) *Lesteva pallipes*, B) *Lesteva longelytra*, C) *Unamis* sp. undescribed, D) *Unamis* sp., E) *Phlaeopterus lagrandeuri*, F) *P. houkae*, G) *P. longipennis*, and H) *P. obsoletus*.

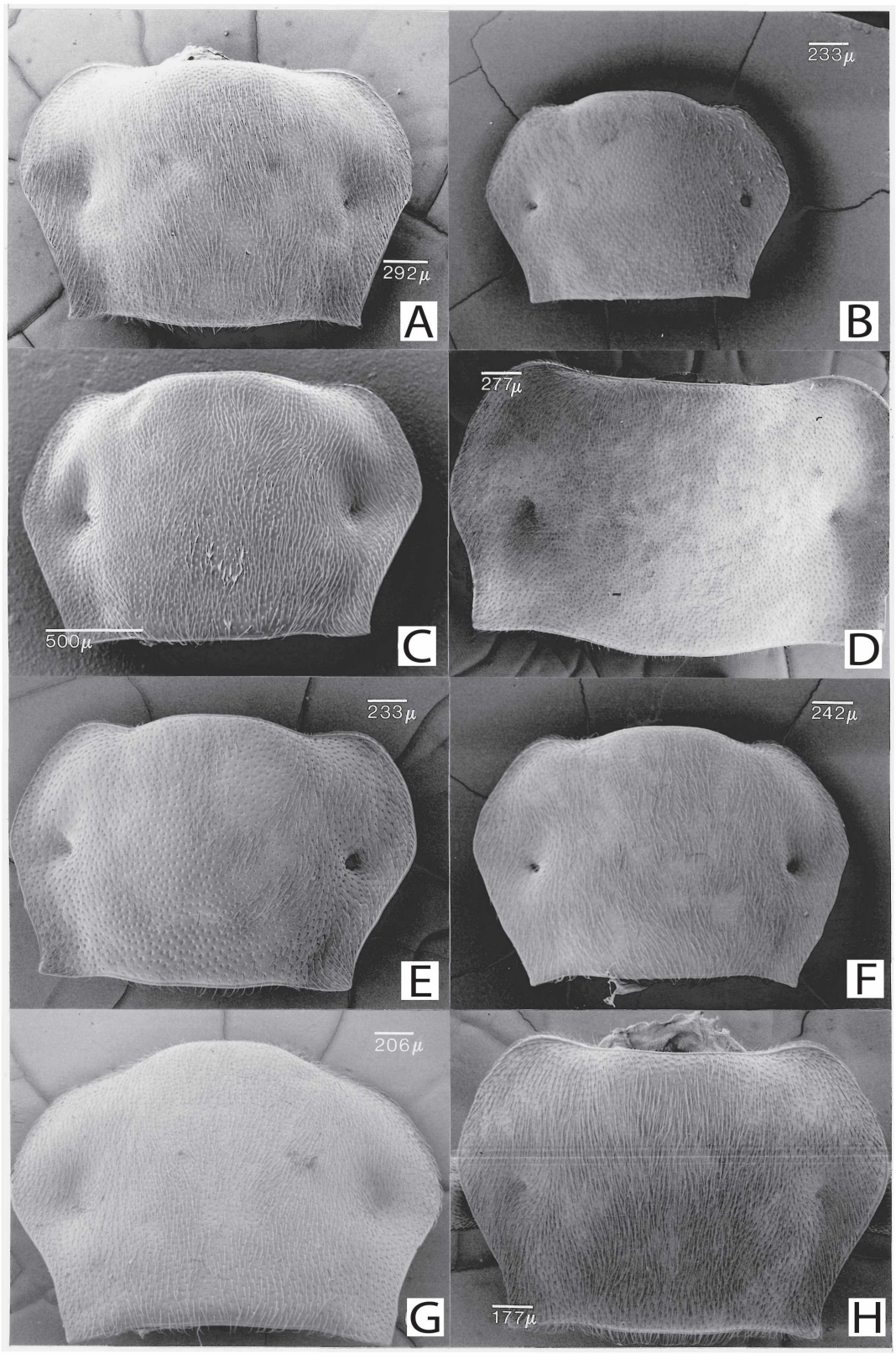

Figure 1.16. Dorsal view of pronotum of A) *Phlaeopterus kavanaughi*, B) *P. castaneus*, C) *P. cavicollis*, D) *P. bakerensis*, E) *P. smetanai*, F) *P. occidentalis*, G) *P. olympicus*, and H) *P. loganensis*.

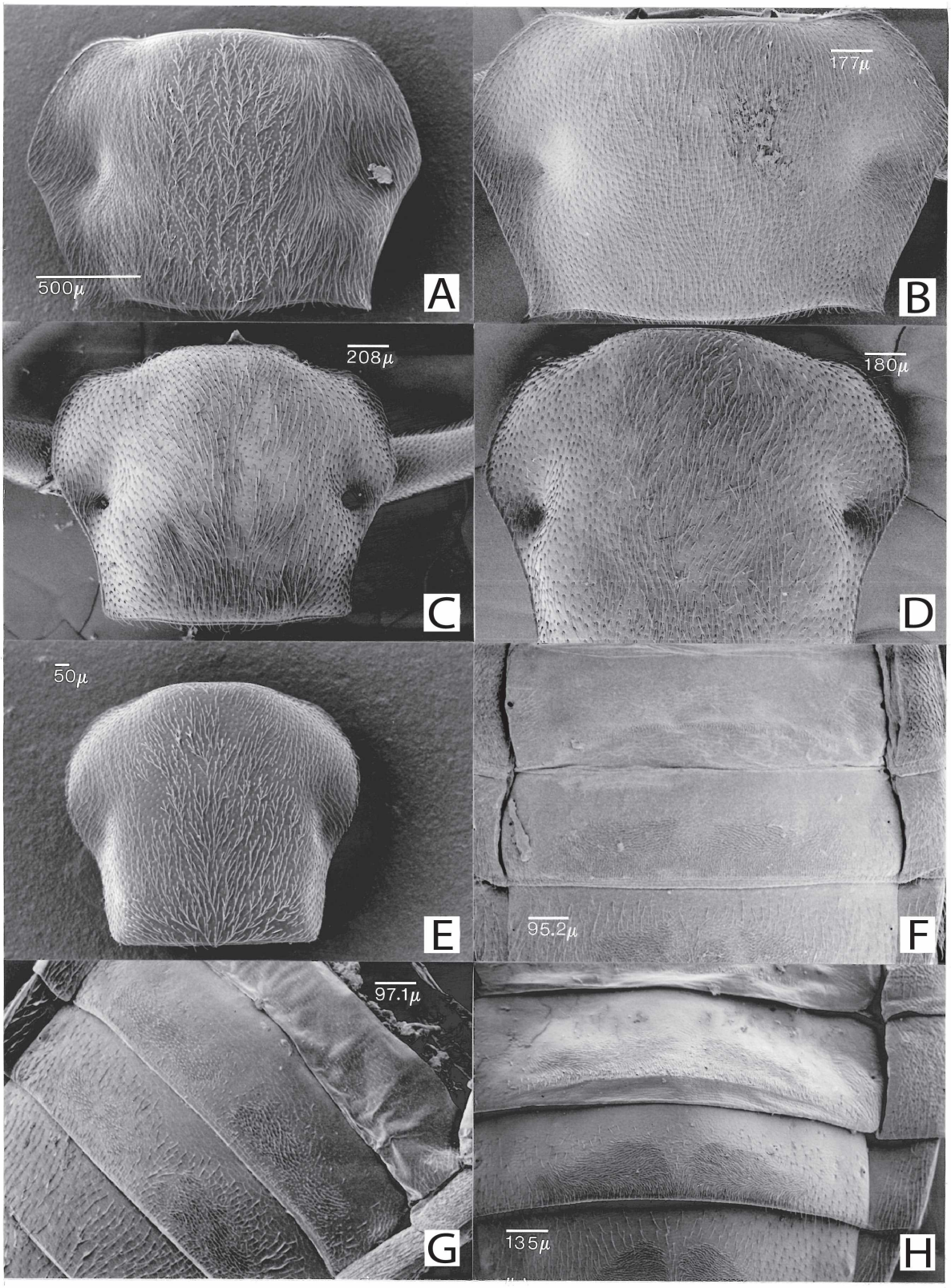

Figure 1.17. Dorsal view of pronotum of A) *Phlaeopterus fusconiger*, B) *P. frosti*, C) *P. filicornis*, D) *P. hatchi*, E) *P. elongatus*, and dorsal view of segments 4–6 of abdomen of F) *P. houkae*, G) *P. obsoletus*, and H) *P. elongatus*.

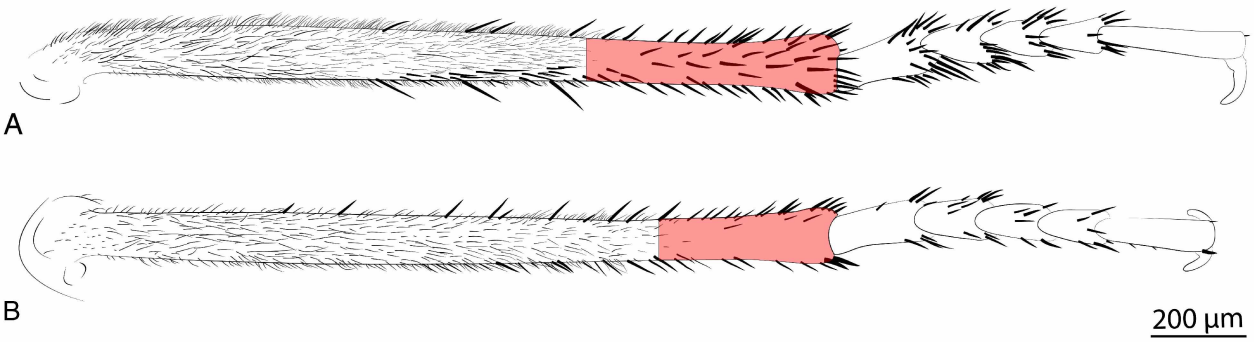

Figure 1.18. Dorsal view of mesotibia of A) *Phlaeopterus frosti* UAM10038755211, and B) *P. fusconiger* UAM100399083. Red highlights are added to emphasize the difference the length of glabrous region (lacking dense pubescence but with longer spine-like setae) at the apex of the tibia.

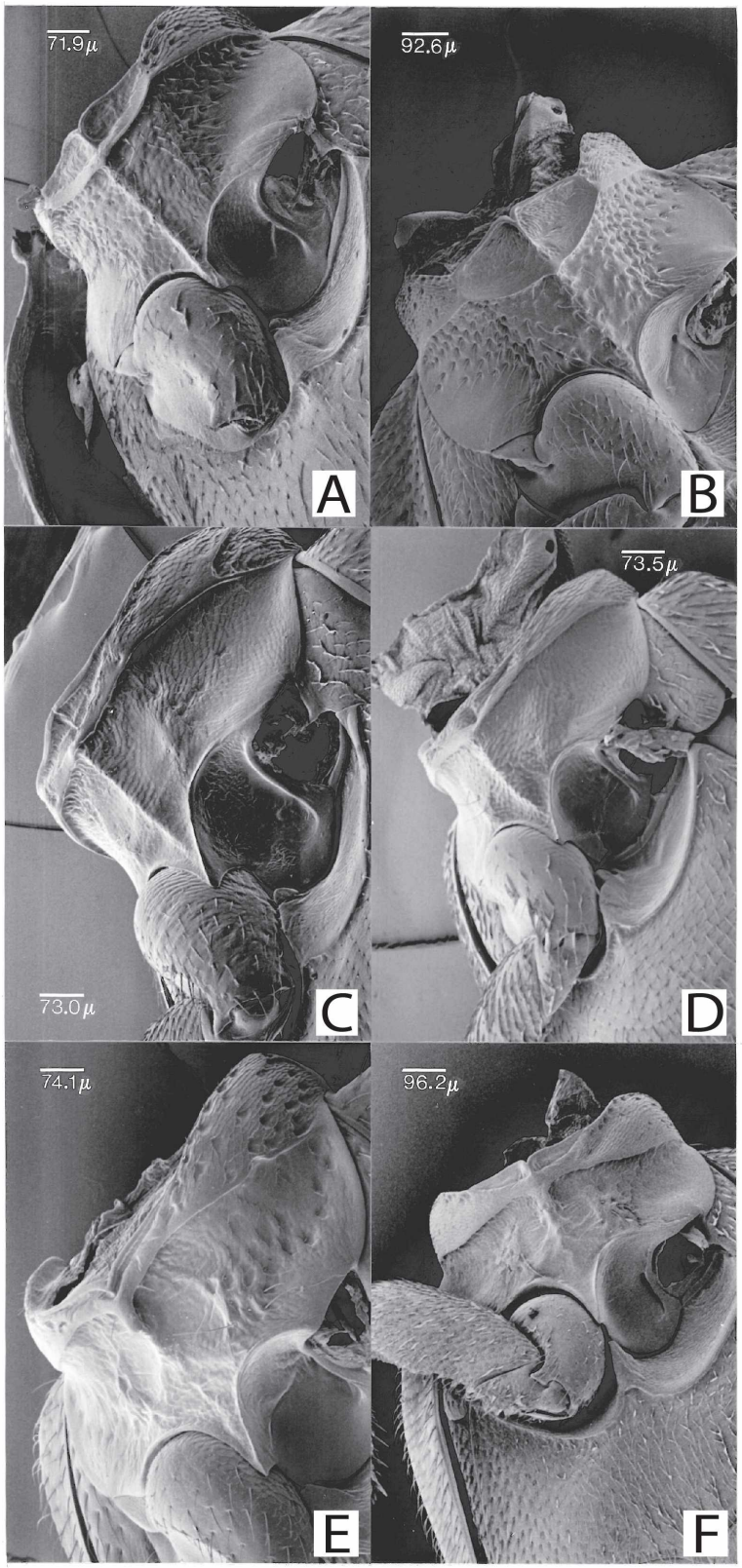

Figure 1.19. Ventral oblique view of mesosternum of A) *Lesteva pallipes*, B) *Lesteva longelytra*, C) *Unamis* sp. undescribed, D) *Unamis sp.*, E) *Phlaeopterus lagrandeuri*, and F) *P. houkae*.

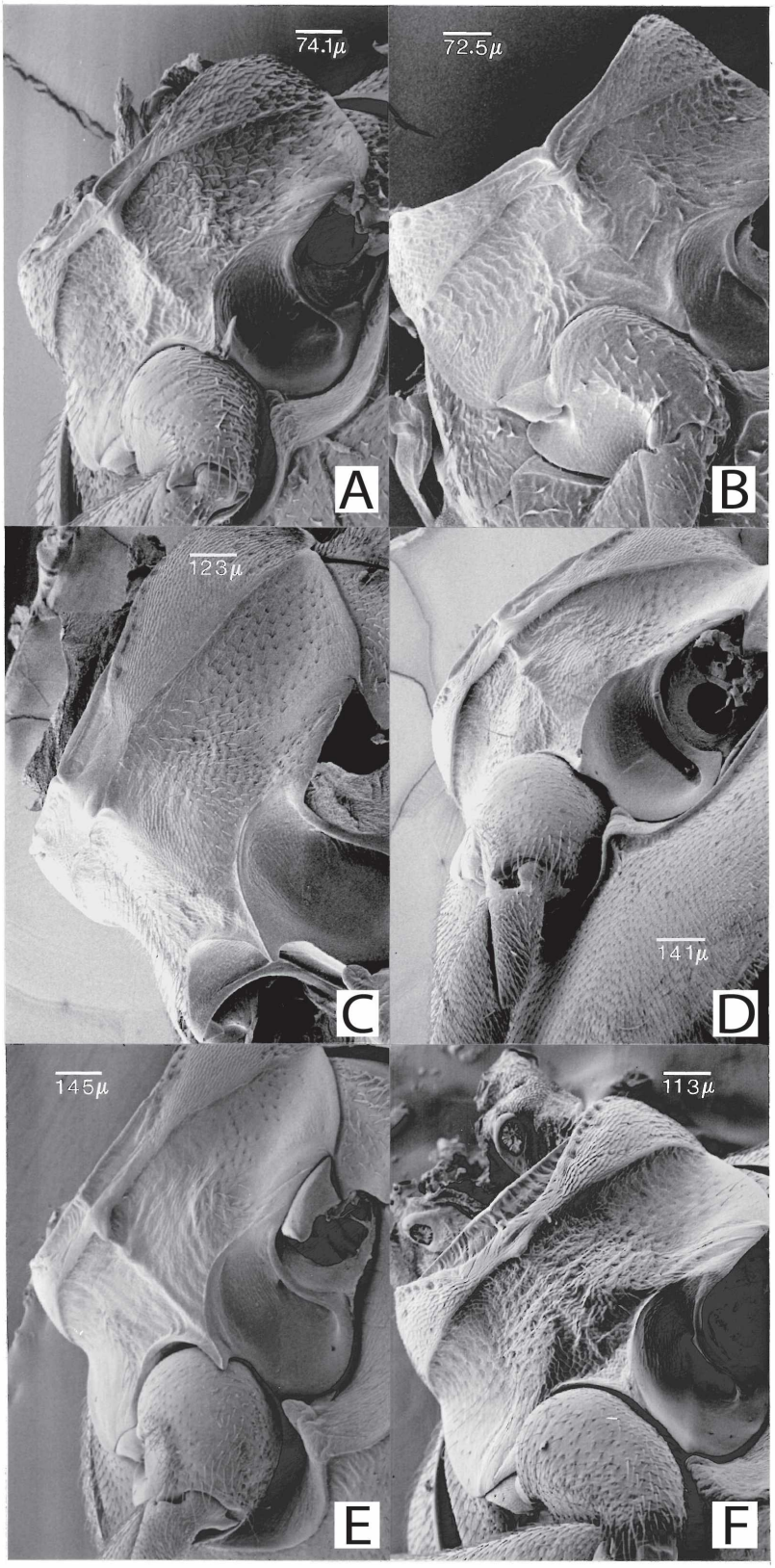

Figure 1.20. Ventral oblique view of mesosternum of A) *Phlaeopterus longipennis*, B) *P. obsoletus,* C) *P. olympicus*, D) *P. frosti*, E) *P. occidentalis*, and F) *P. elongatus*.

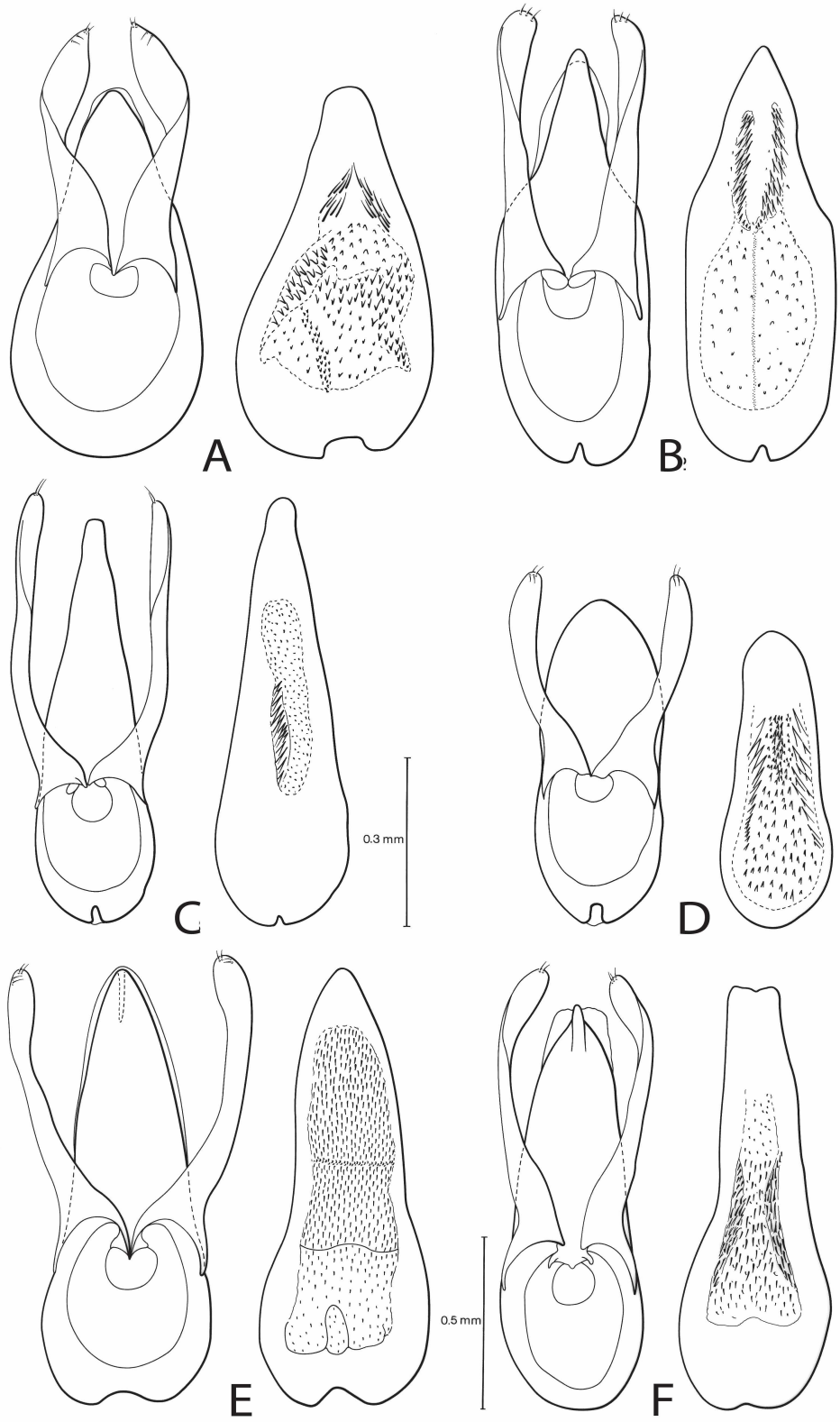

Figure 1.21. Aedeagus (left, ventral view; right, dorsal view of median lobe) of A) *Phlaeopterus lagrandeuri*, B) *P. houkae*, C) *P. longipennis*, D) *P. frosti*, E) *P. bakerensis*, and F) *P. castaneus cascadiensis*.

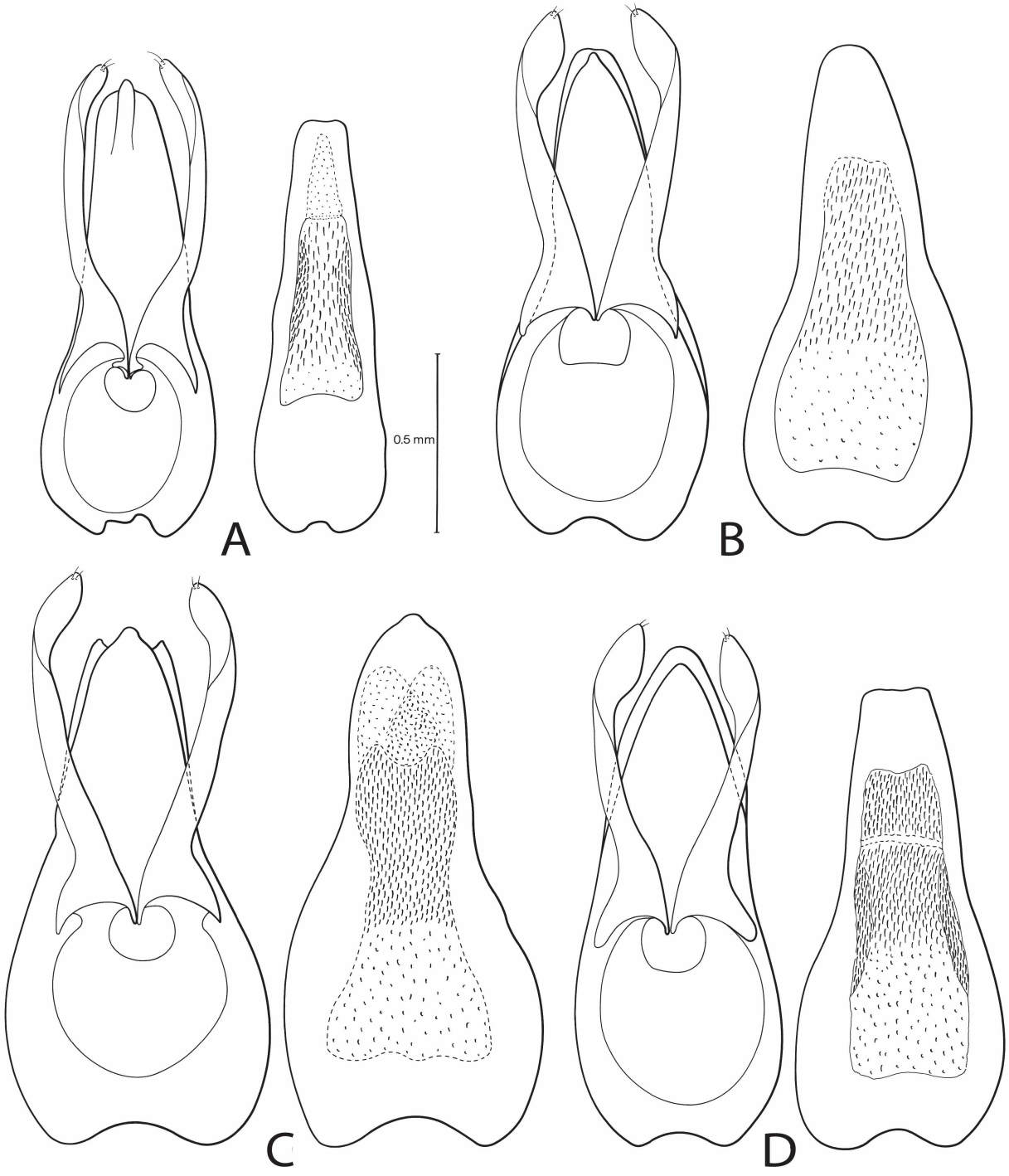

Figure 1.22. Aedeagus (left, ventral view; right, dorsal view of median lobe) of A) *Phlaeopterus castaneus castaneus*, and variation in the aedeagus of *P. cavicollis*: B), C), and D).

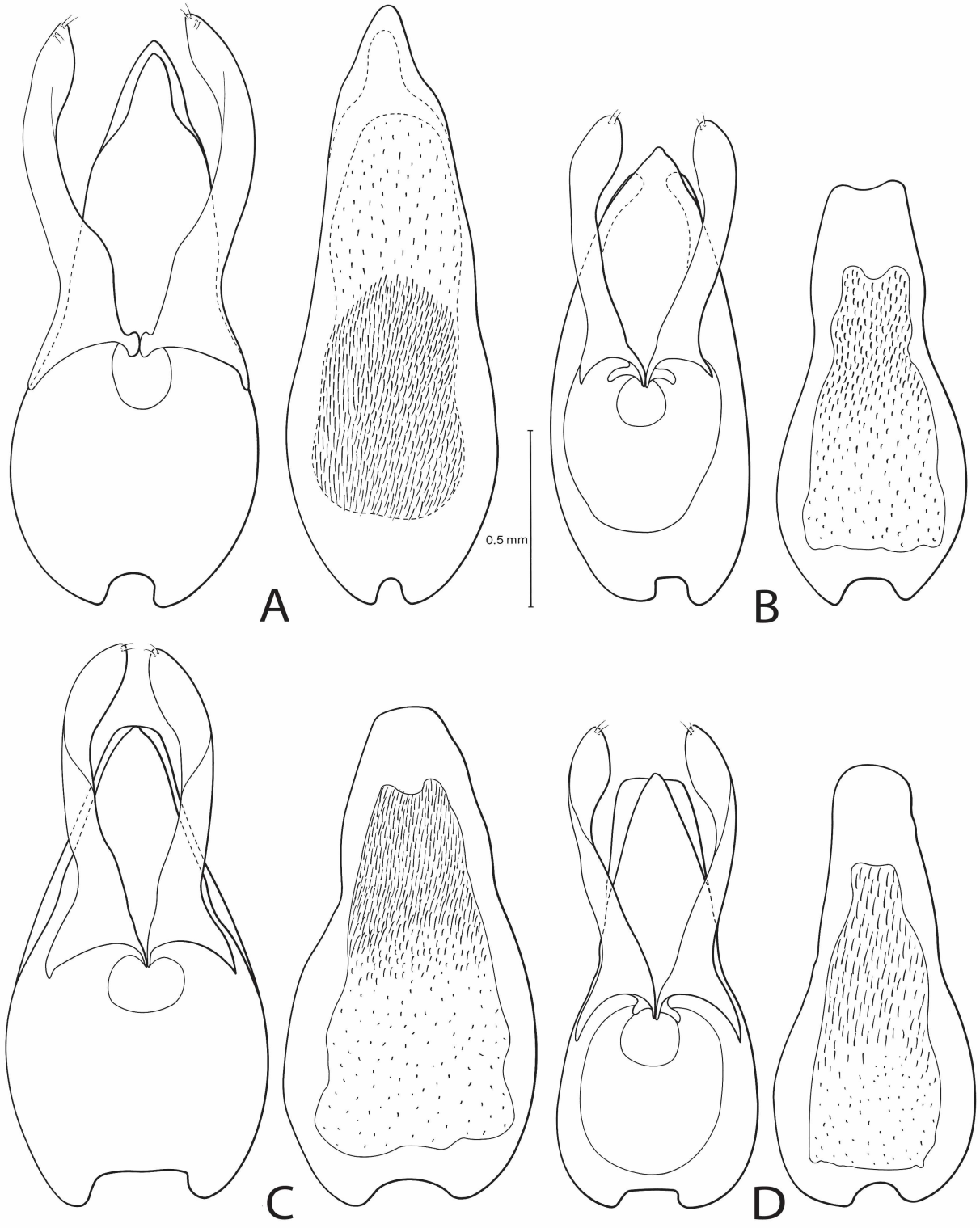

Figure 1.23. Aedeagus (left, ventral view; right, dorsal view of median lobe) of A) *Phlaeopterus bakerensis*, B) *P. smetanai*, C) *P. smetanai*, and D) *P. occidentalis*.

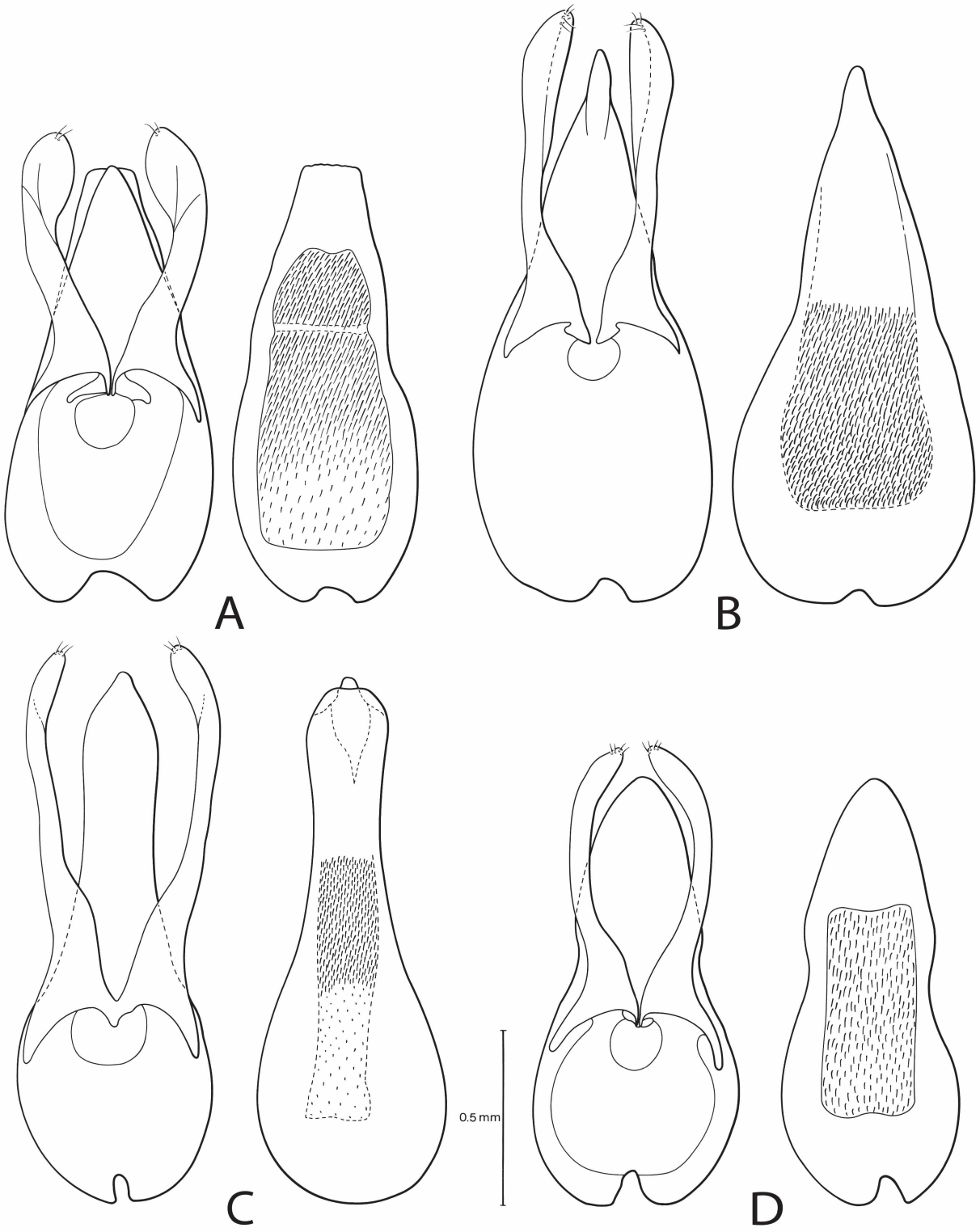

Figure 1.24. Aedeagus (left, ventral view; right, dorsal view of median lobe) of A) *Phlaeopterus occidentalis*, B) *P. olympicus*, C) *P. loganensis*, and D) *P. fusconiger*.

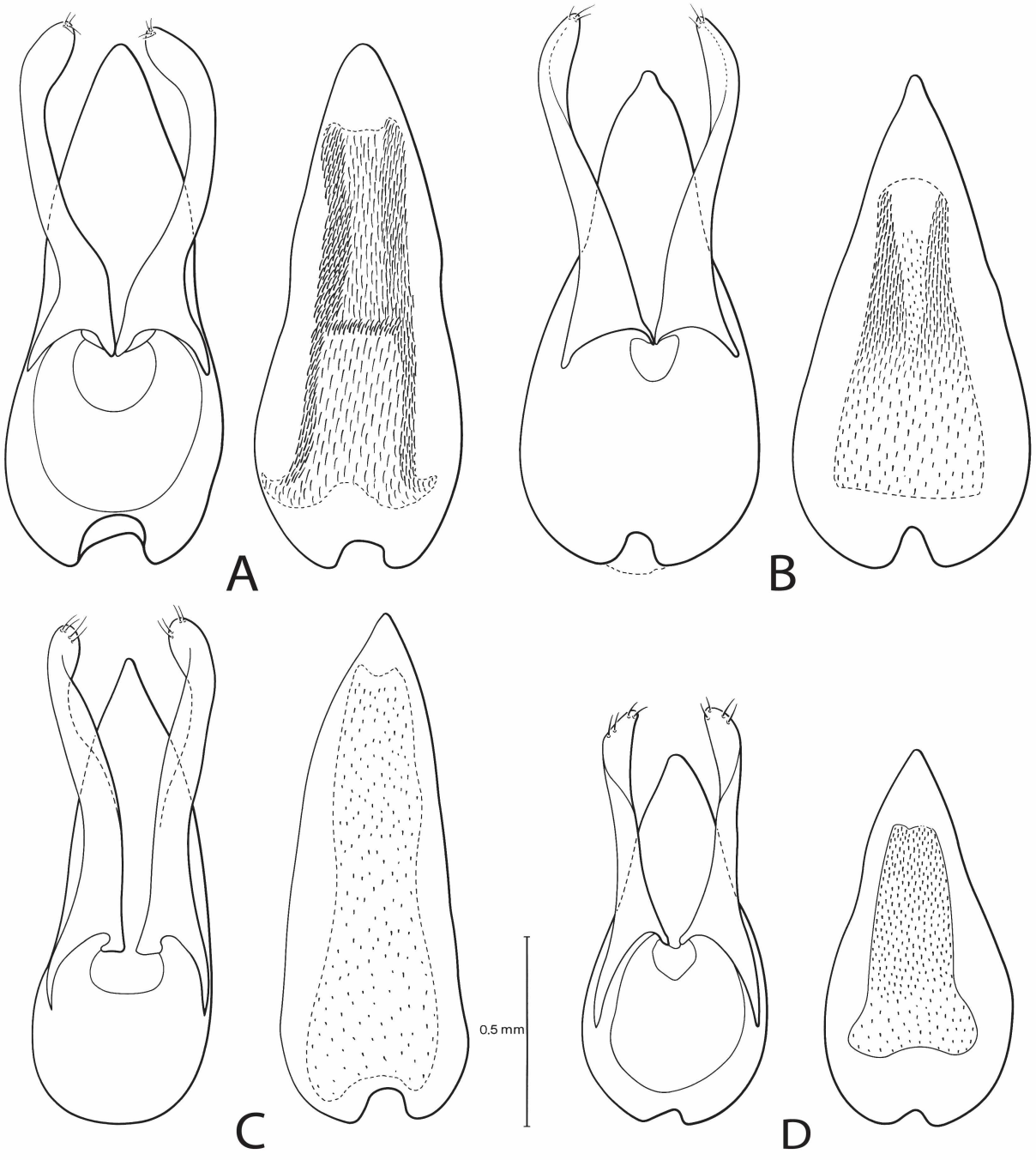

Figure 1.25. Aedeagus (left, ventral view; right, dorsal view of median lobe) of A) *Phlaeopterus frosti*, B) *P. filicornis*, C) *P. hatchi*, and D) *P. elongatus*.

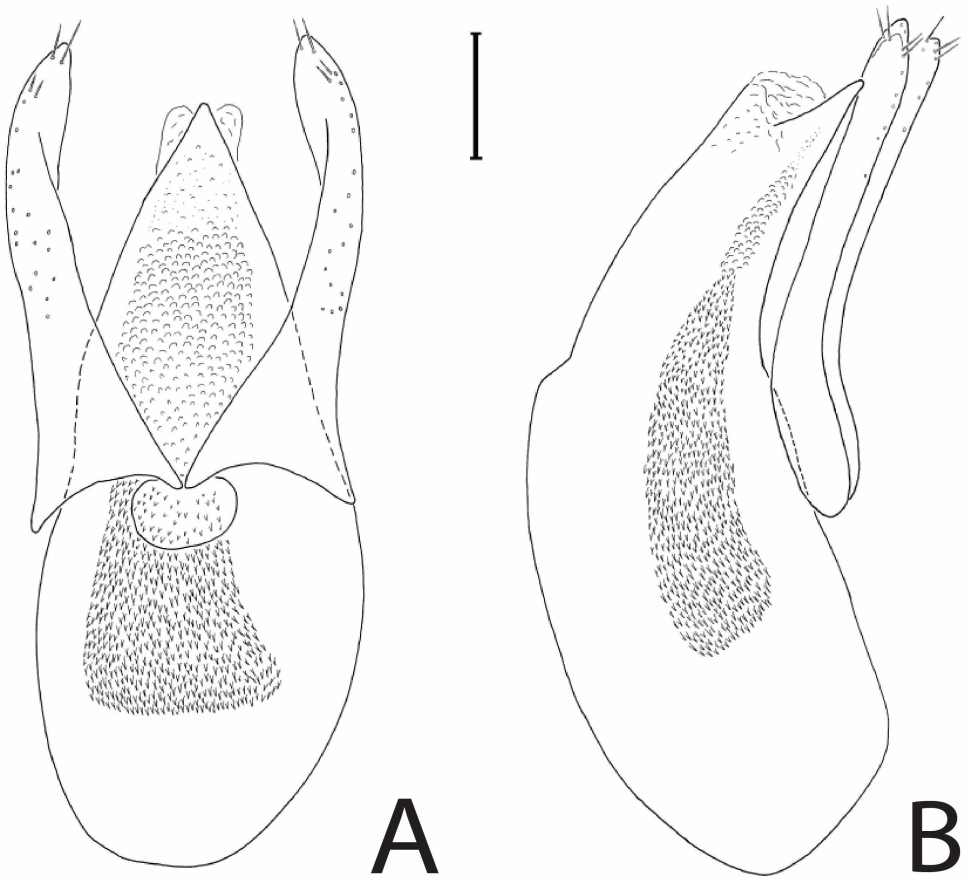

Figure 1.26. Aedeagus of *Phlaeopterus czerskyi* A) ventral view, and B) lateral view. Scale bar = 0.1 mm.

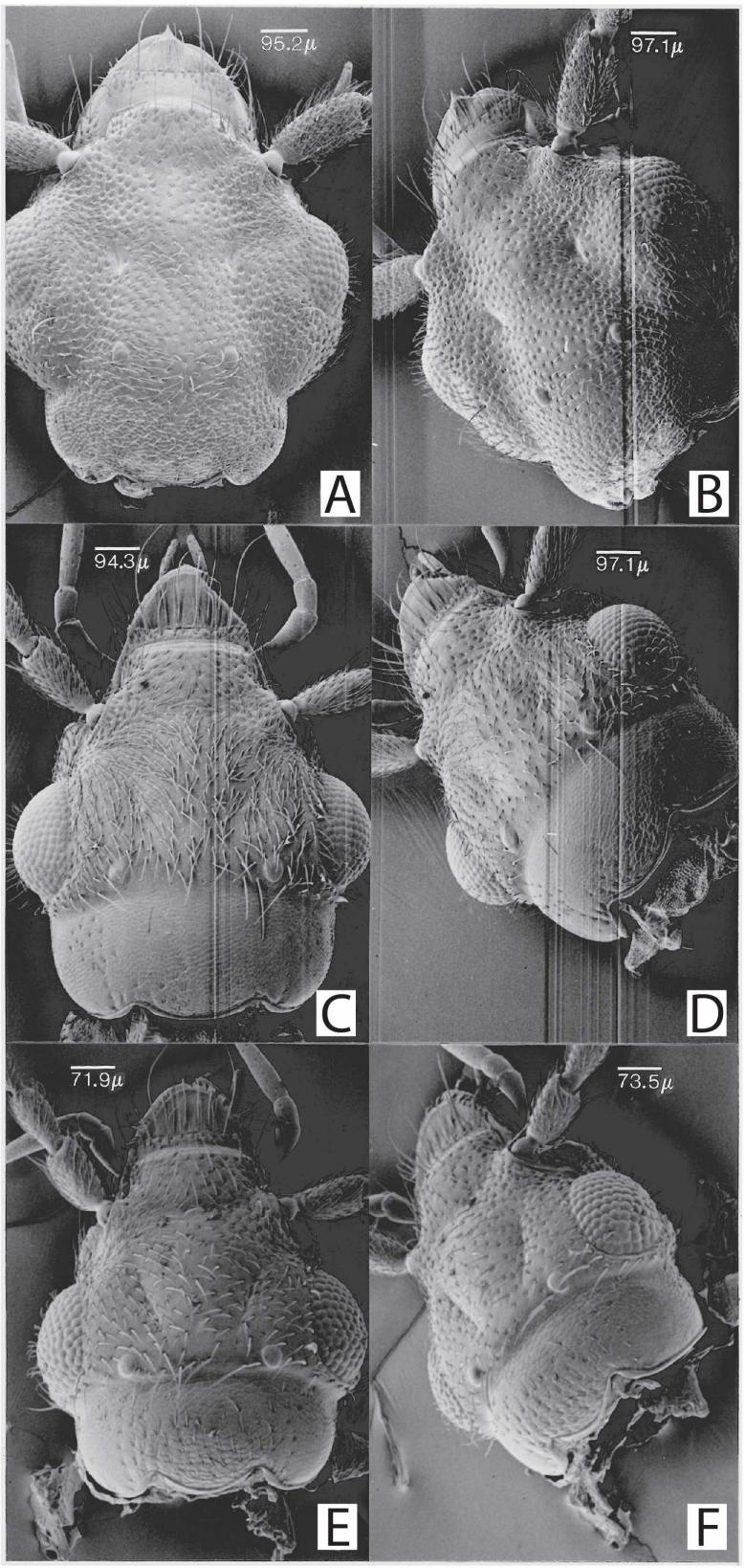

Figure 1.27. Dorsal and dorsal oblique view of head of A) and B) *Lesteva pubescens*, C) and D) *Unamis* sp. undescribed, E) and F) *Unamis* sp.

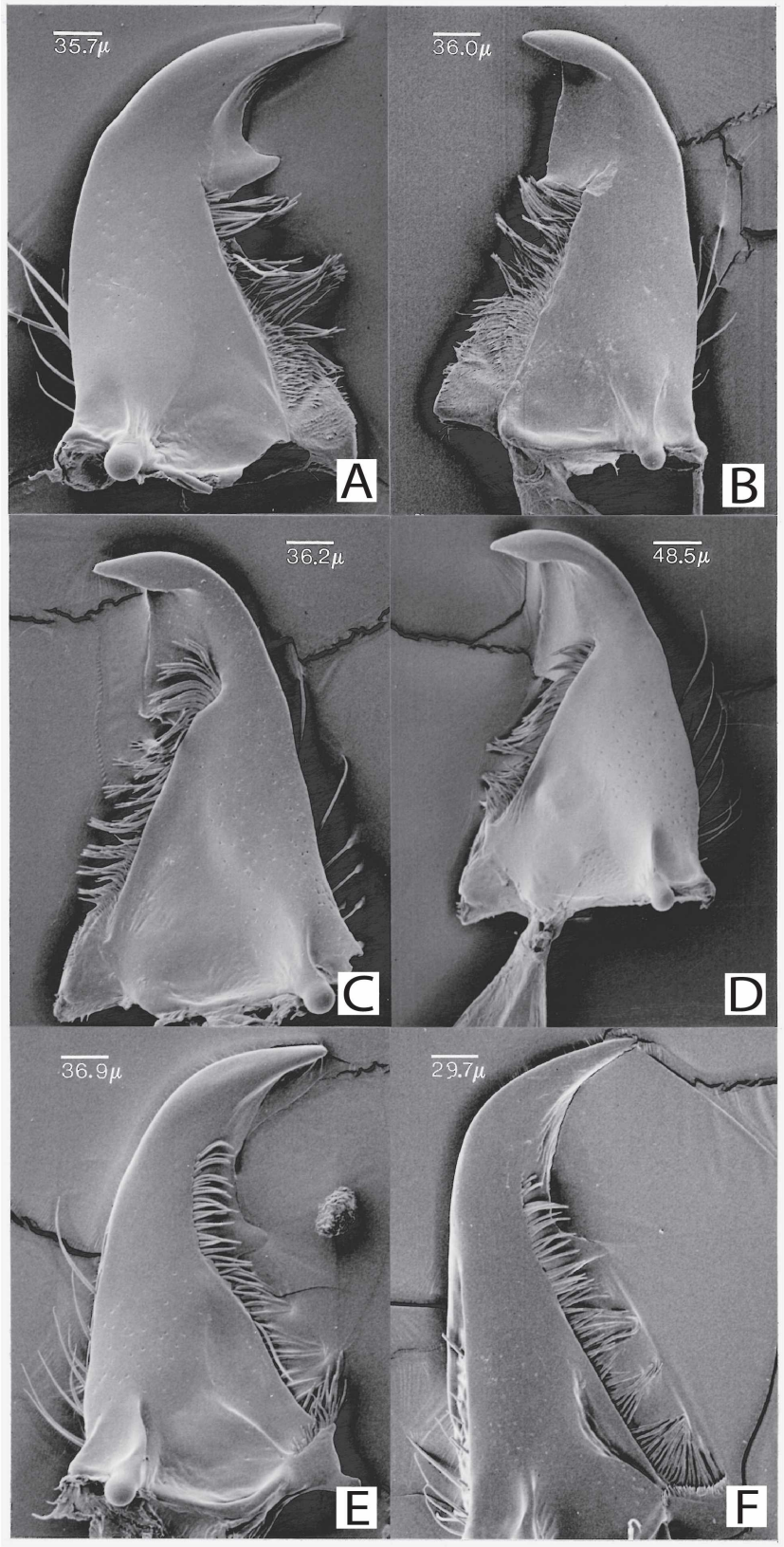

Figure 1.28. Ventral view of mandible of A) *Lesteva longelytra*, B) *Lesteva pallipes*, C) *Unamis* sp. undescribed, D) *Unamis* sp., E) *Phlaeopterus lagrandeuri*, F) *P. houkae*.

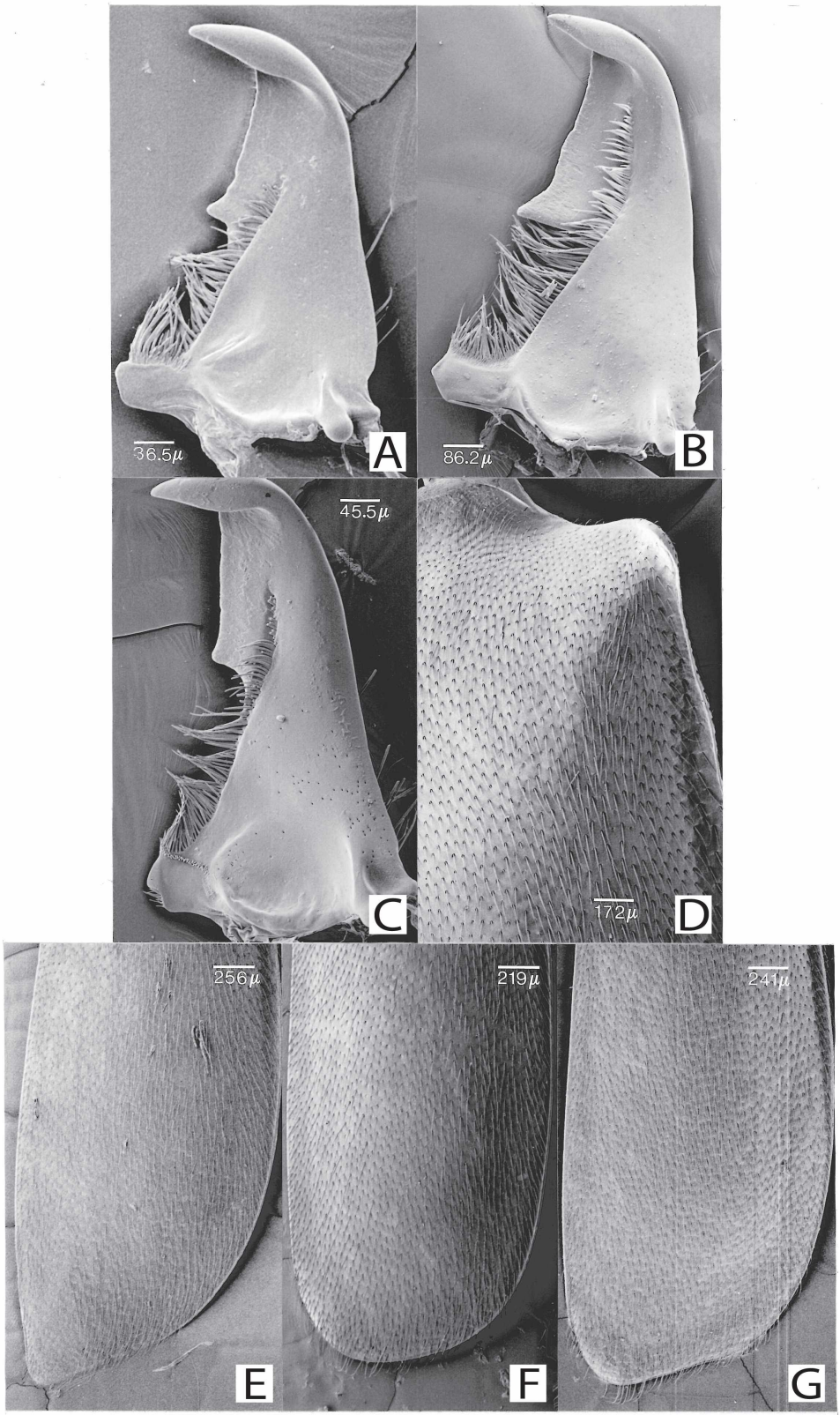

Figure 1.29. Ventral view of mandible of A) *Phlaeopterus obsoletus*, B) *P. bakerensis*, C) *P. elongatus*, D) dorsal view of humeral angle of elytra of *P. bakerensis*, E) apex of elytra of *P. loganensis*, F) apex of elytra of *P. hatchi*, and G) apex of elytra of *P. filicornis*.

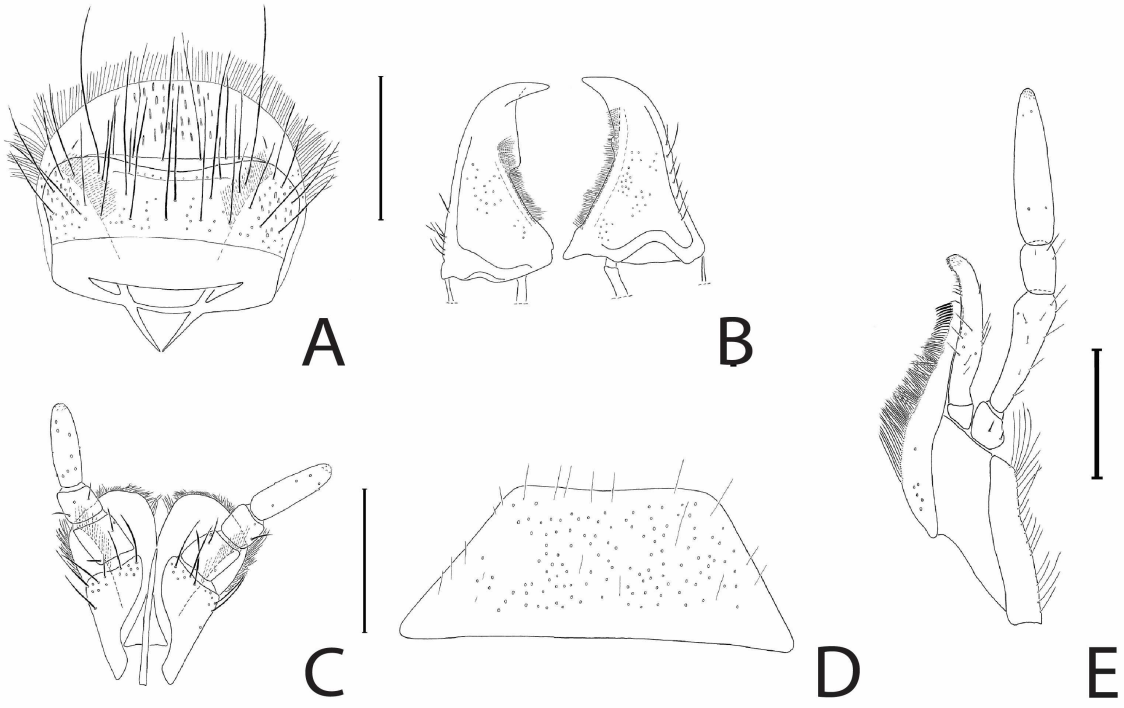

Figure 1.30. Mouthparts of *Phlaeopterus czerskyi*: A) dorsal view of labium, B) dorsal view of labrum, C) dorsal view of mandibles, D) dorsal view of right maxilla, and E) dorsal view of mentum. Scale bars = 0.1 mm.

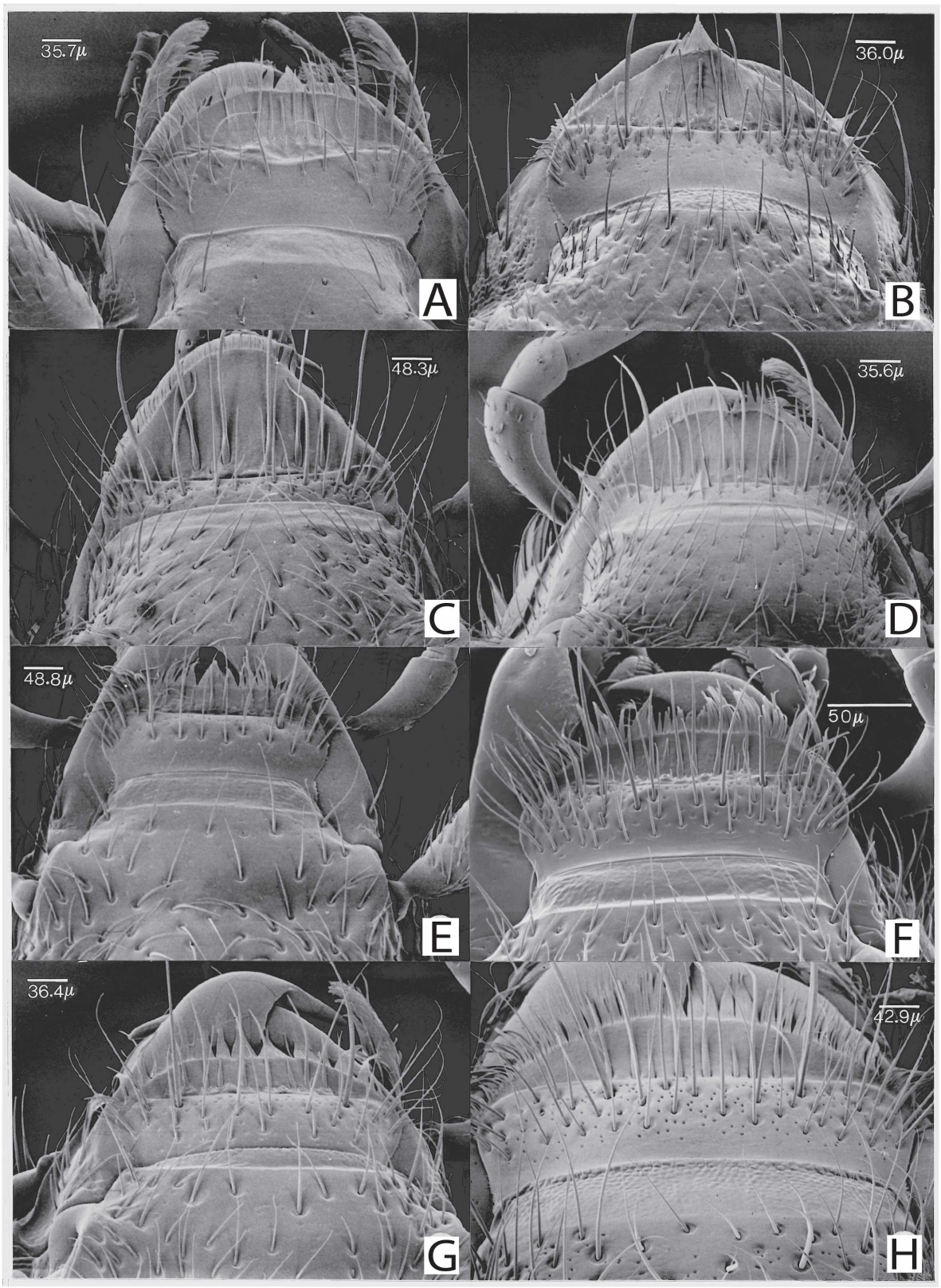

Figure 1.31. Labrum of A) *Lesteva pallipes*, B) *Lesteva pubescens*, C) *Unamis* sp, undescribed, and D) *Unamis* sp., E) *Phlaeopterus lagrandeuri*, F) *P. houkae*, G) *P. obsoletus*, H) *P. filicornis*.

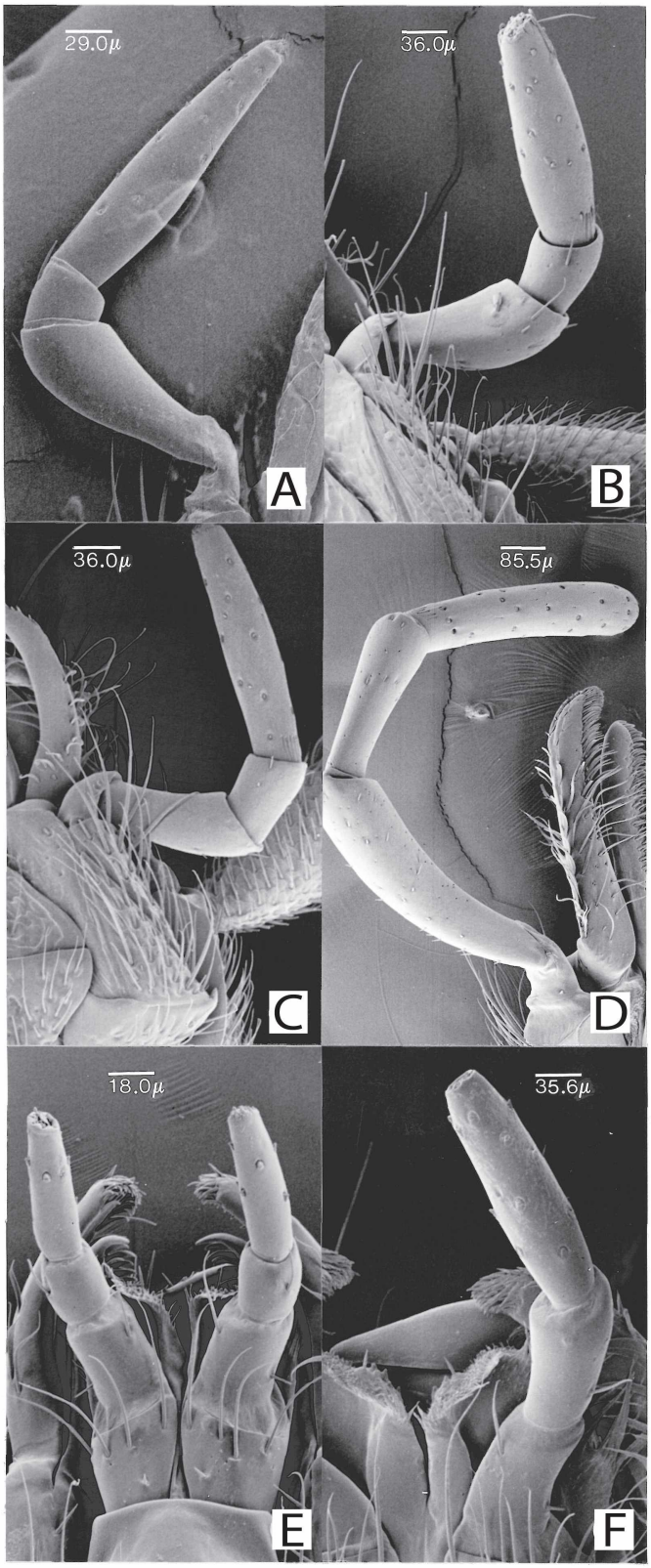

Figure 1.32. Dorsal and ventral views of maxilla of A) and B) *Lesteva longelytra*, C) and D) *Unamis* sp. undescribed, E) and F) *Phlaeopterus lagrandeuri*, G) and H) *P. houkae*, I) and J) *P. obsoletus*, K) and L) *P. elongatus*.

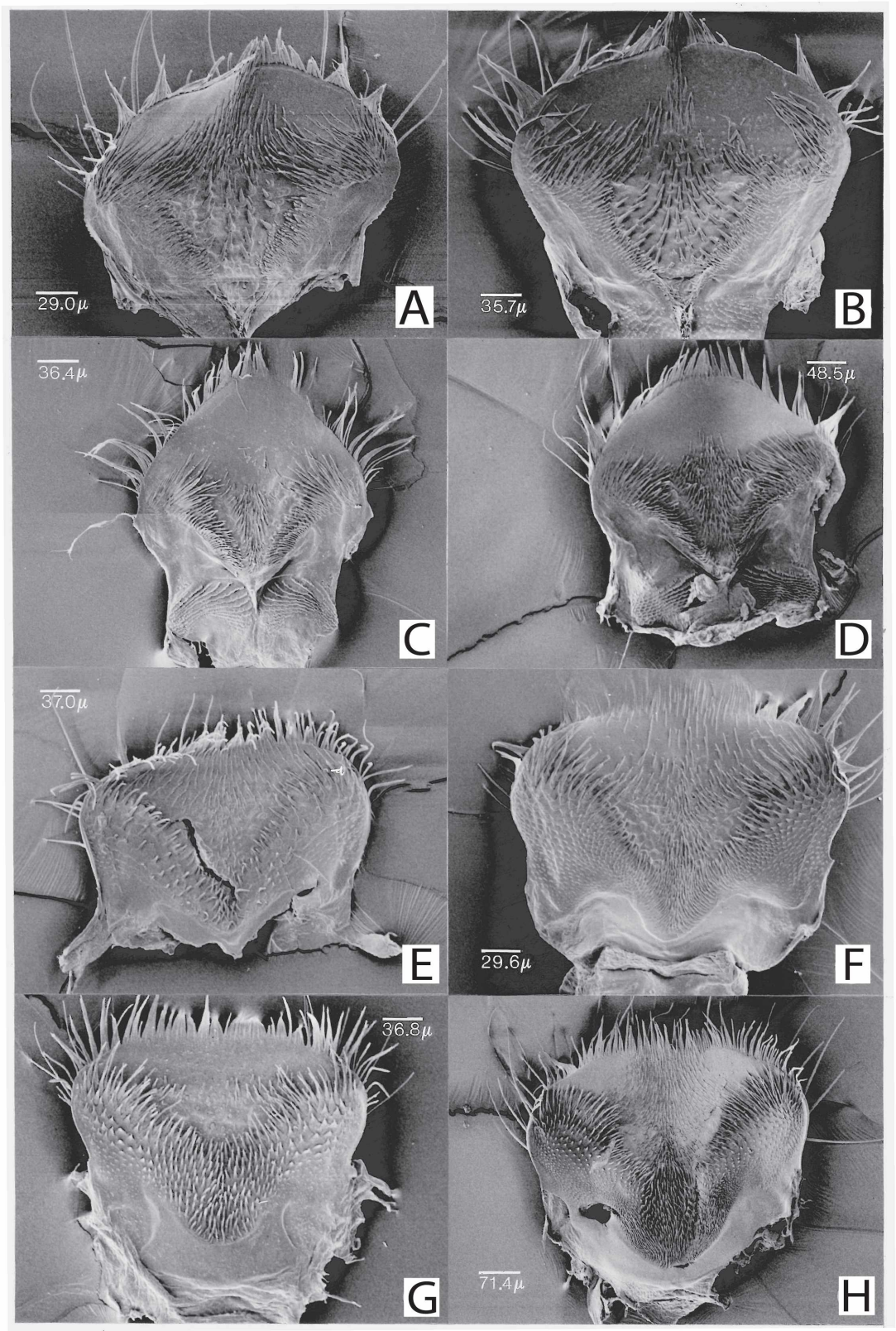

Figure 1.33. Epipharynx of A) *Lesteva pallipes*, B) *Lesteva longelytra*, C) *Unamis* sp. undescribed, D) *Unamis* sp., E) *Phlaeopterus lagrandeuri*, F) *P. houkae*, G) *P. obsoletus*, and H) *P. smetanai*.

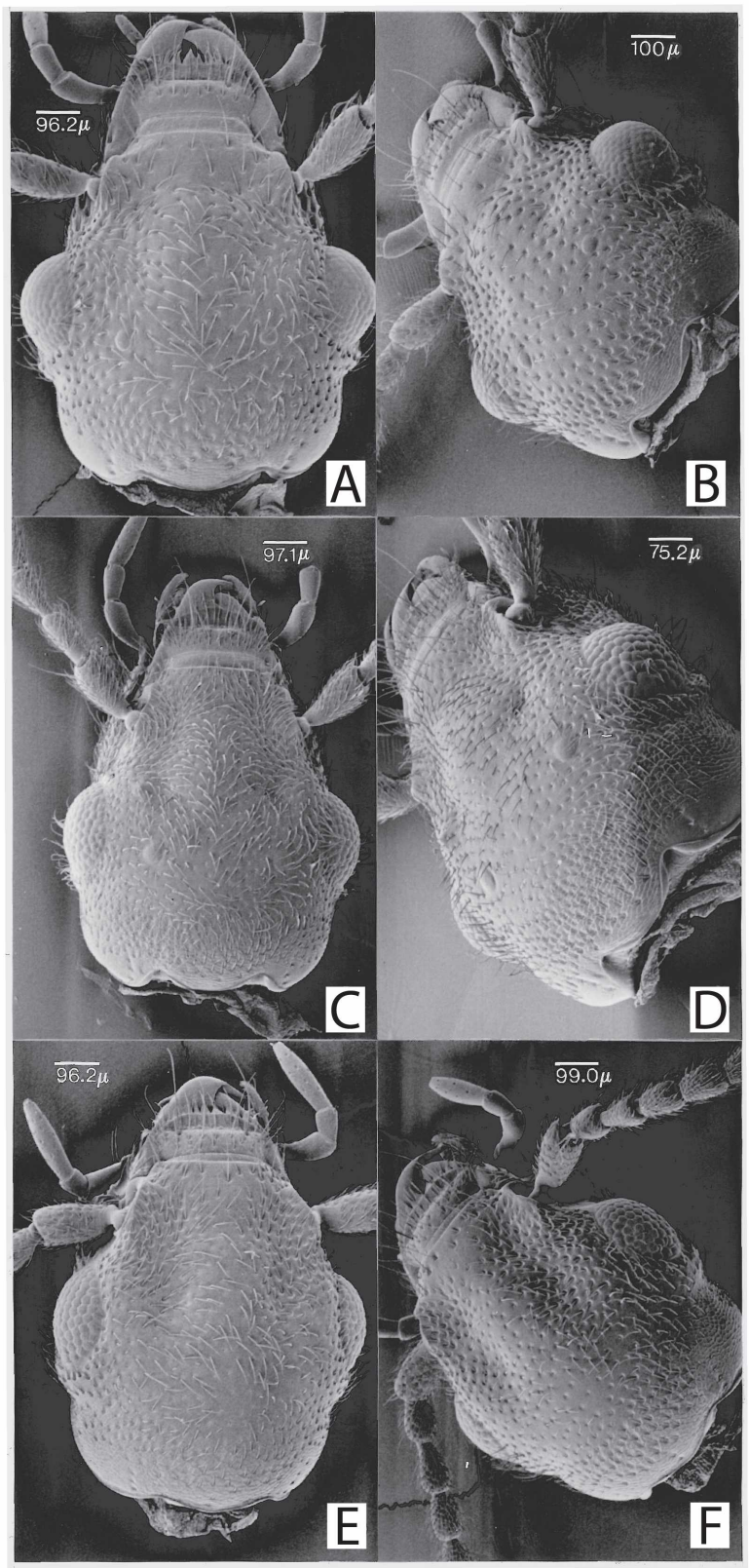

Figure 1.34. Dorsal and dorsal oblique view of head of A) and B) *Phlaeopterus lagrandeuri*, C) and D) *P. houkae*, E) and F) *P. obsoletus*, G) and H) *P. kavanaughi*, I) and J) *P. hatchi*, and dorsal view of the eye of K) *Lesteva longelytra*, and L) *Unamis* sp. undescribed.

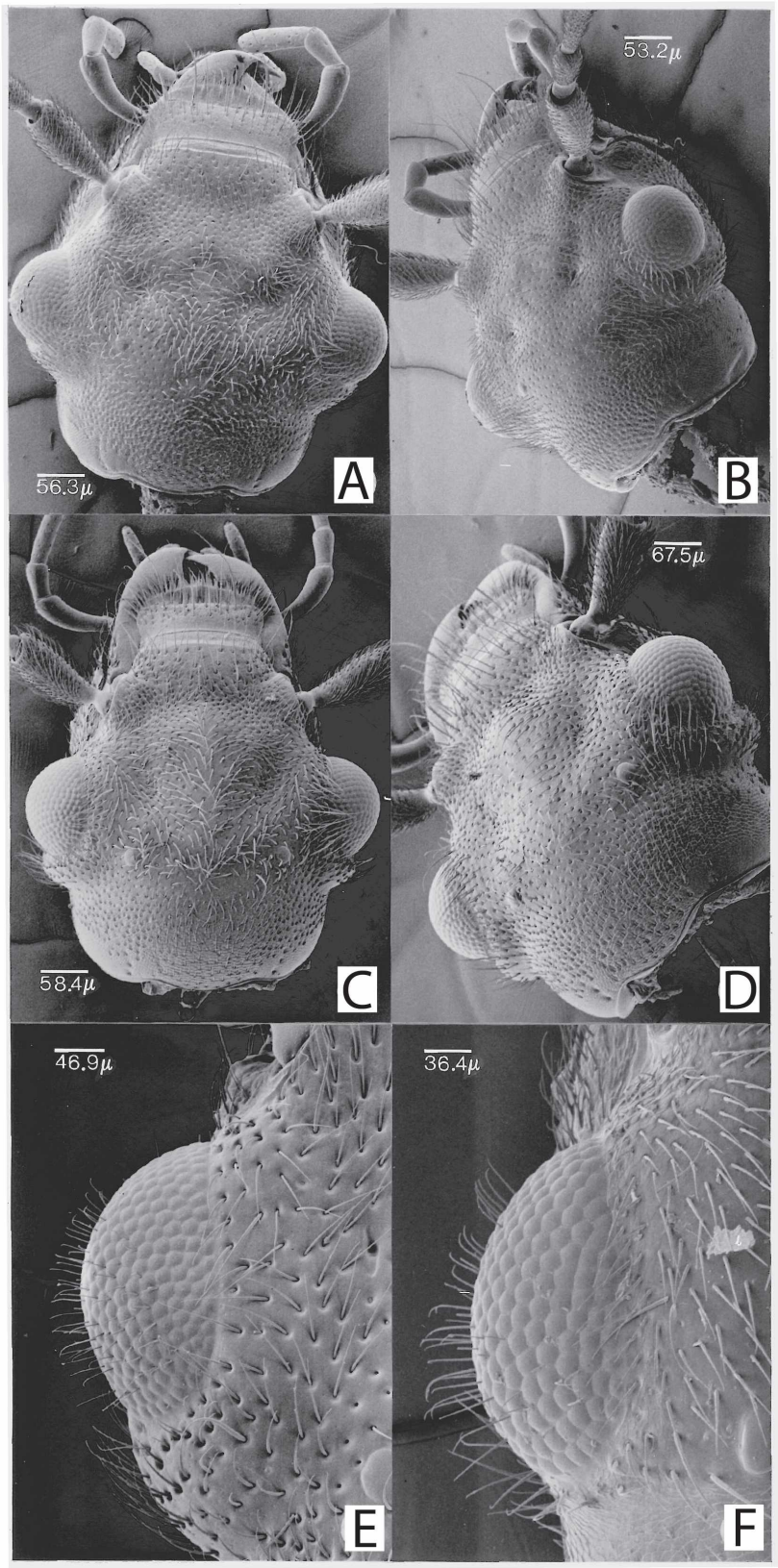

Figure 1.35. Dorsal and dorsal oblique view of head of A) and B) *Phlaeopterus kavanaughi*, C) and D) *P. hatchi*, and dorsal view of the eye of E) and F) *Lesteva longelytra*.

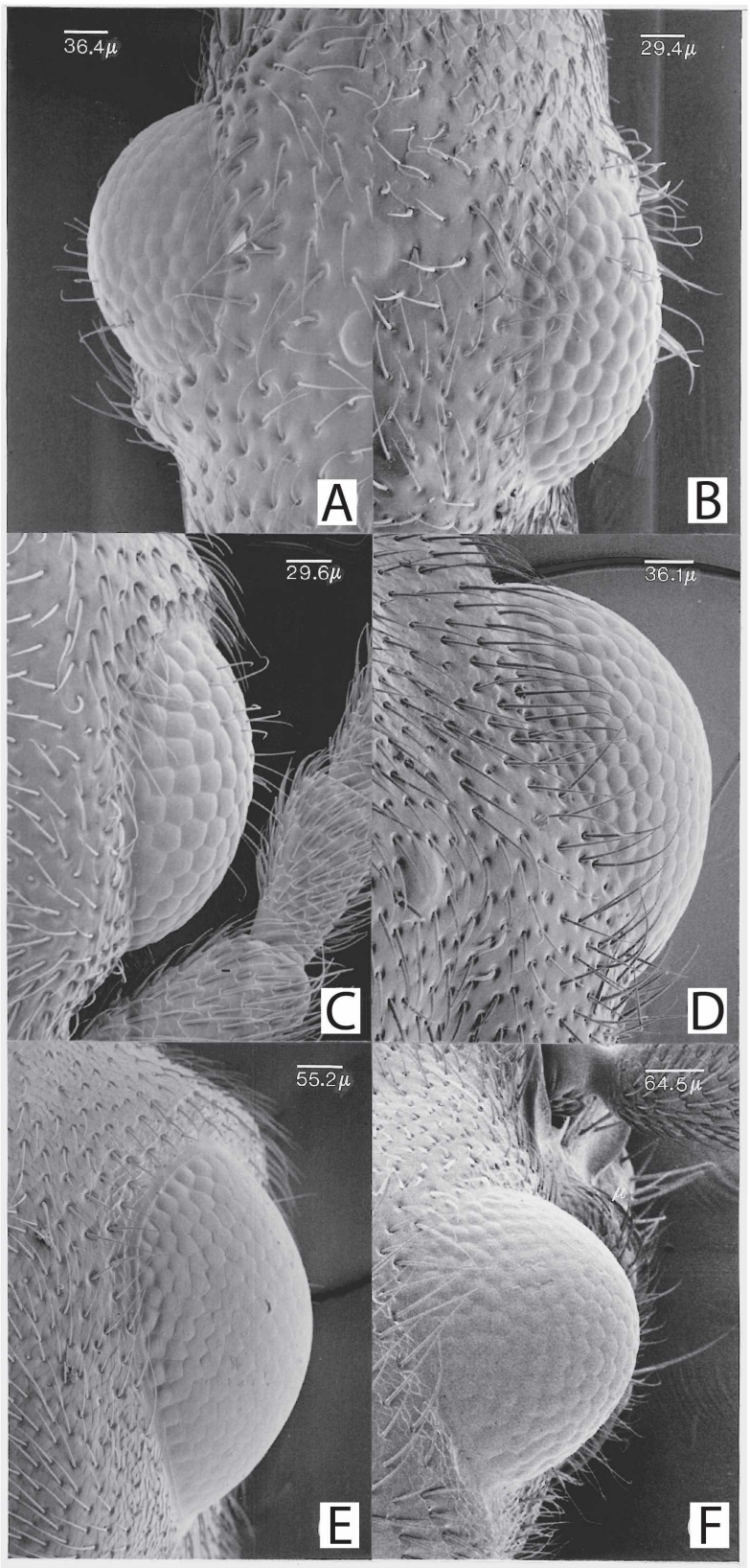

Figure 1.36. Dorsal view of the eye of A) *Phlaeopterus lagrandeuri*, B) *P. houkae*, C) *P. longipennis*, D) *P. frosti*, E) *P. bakerensis*, and F) *P. olympicus*.

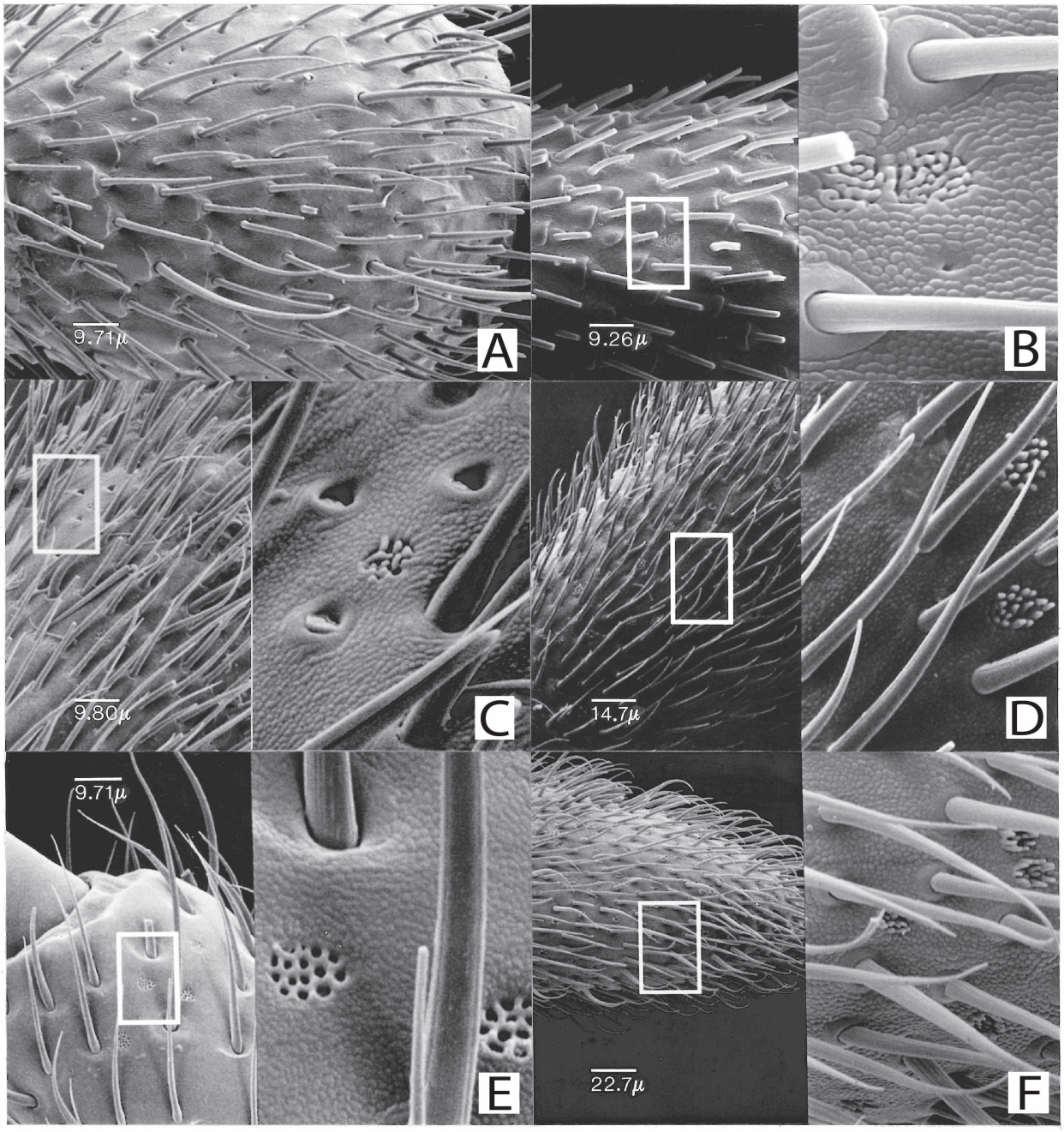

Figure 1.37. Sensory structure of antennae of A) *Lesteva pallipes*, B) *Lesteva pubescens*, C) *Unamis* sp. undescribed, D) *Phlaeopterus houkae*, E) *P. obsoletus*, F) *P. elongatus*.

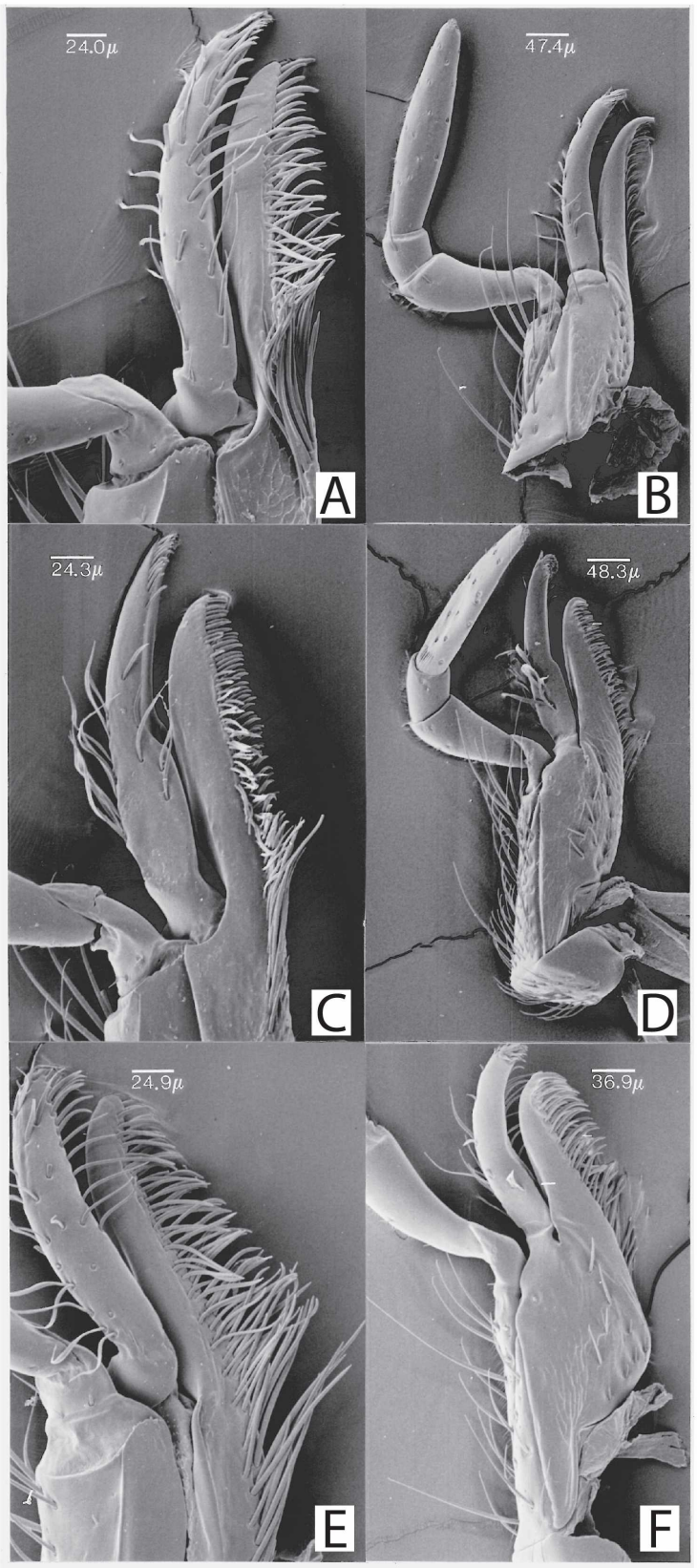

Figure 1.38. Dorsal and ventral views of maxilla of A) and B) *Lesteva longelytra*, C) and D) *Unamis* sp. undescribed, and E) and F) *Phlaeopterus lagrandeuri*.

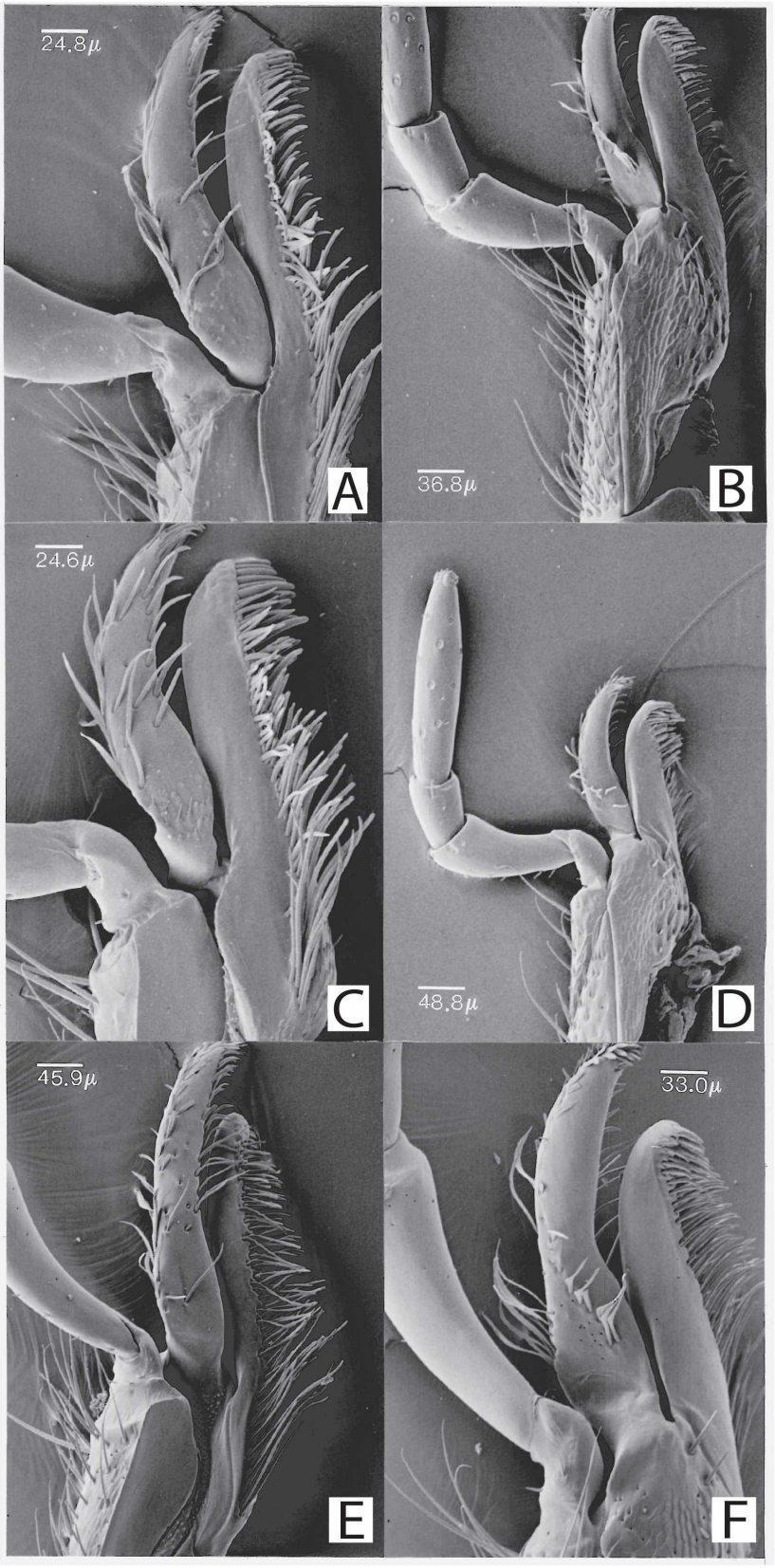

Figure 1.39. Dorsal and ventral views of maxilla of A) and B) *Phlaeopterus houkae*, C) and D) *P. obsoletus*, and E) and F) *P. elongatus*.

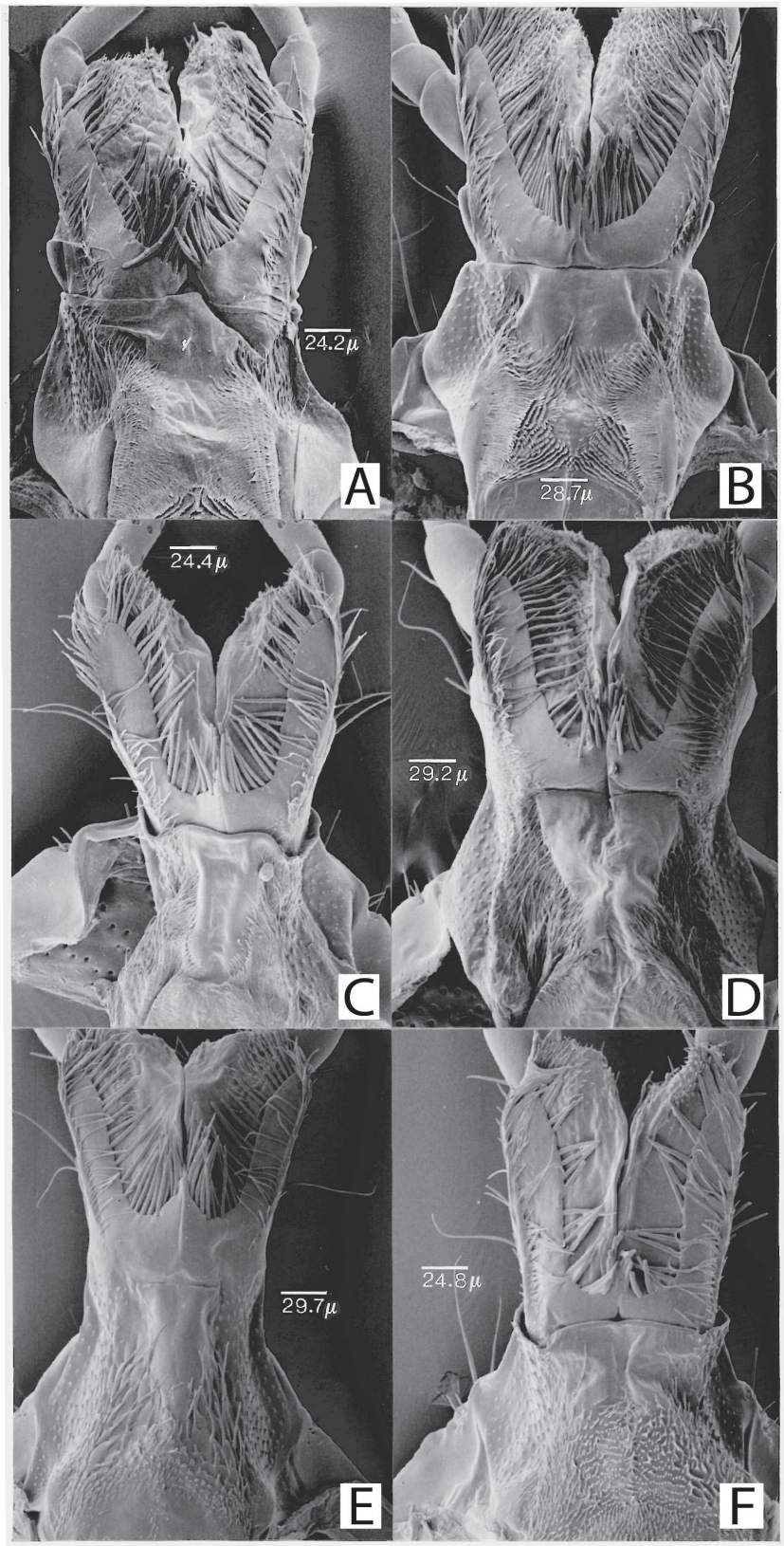

Figure 1.40. Hypopharynx of A) *Lesteva pallipes*, B) *Lesteva longelytra*, C) *Unamis* sp. undescribed, D) *Unamis* sp., E) *Phlaeopterus lagrandeuri*, and F) *P. houkae*.

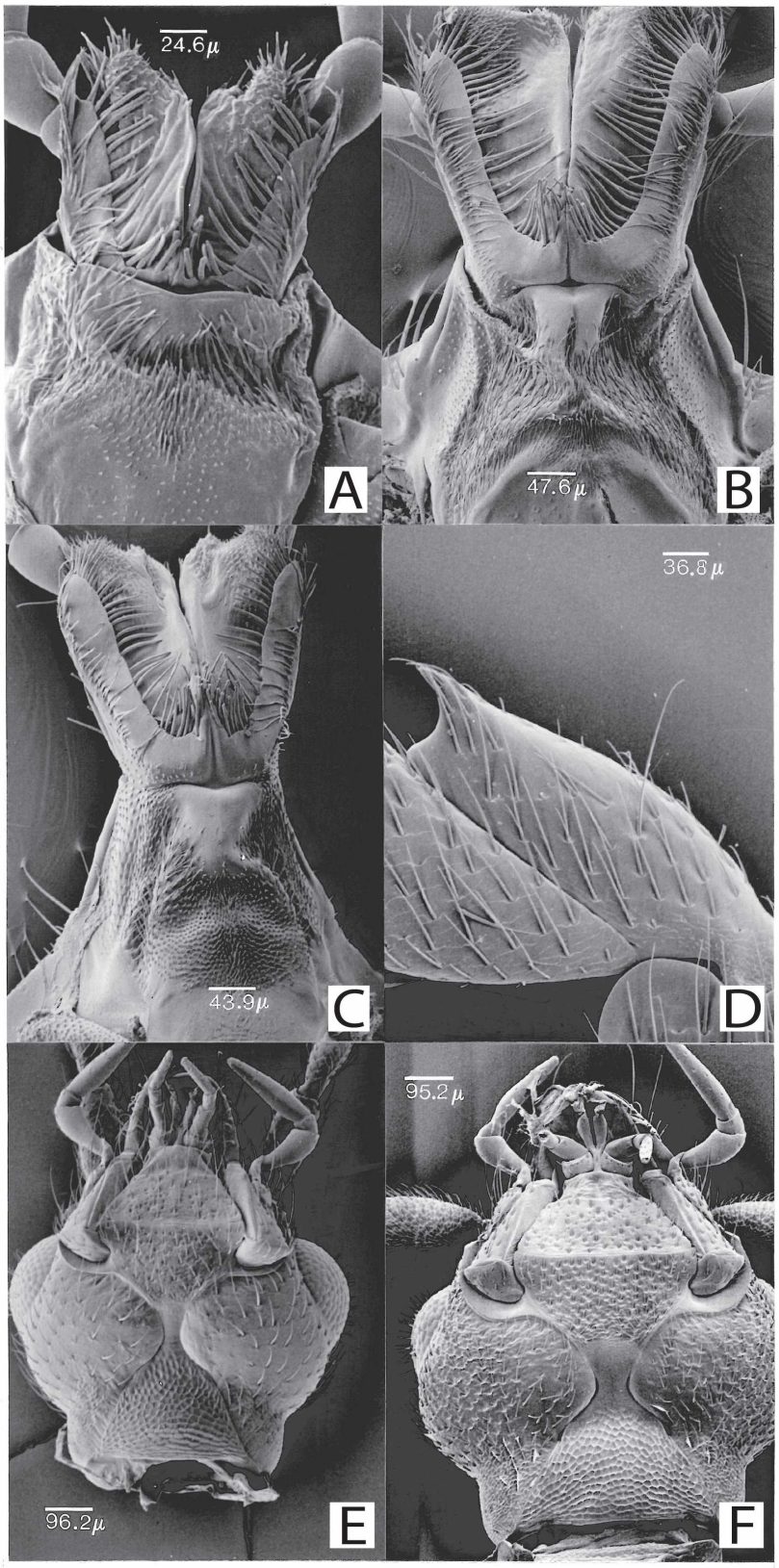

Figure 1.41. Hypopharynx of A) *Phlaeopterus obsoletus*, B) *P. kavanaughi*, C) *P. elongatus*, D) *P. lagrandeuri*, and ventral view of head of E) *Lesteva pallipes*, and F) *Lesteva pubescenes*

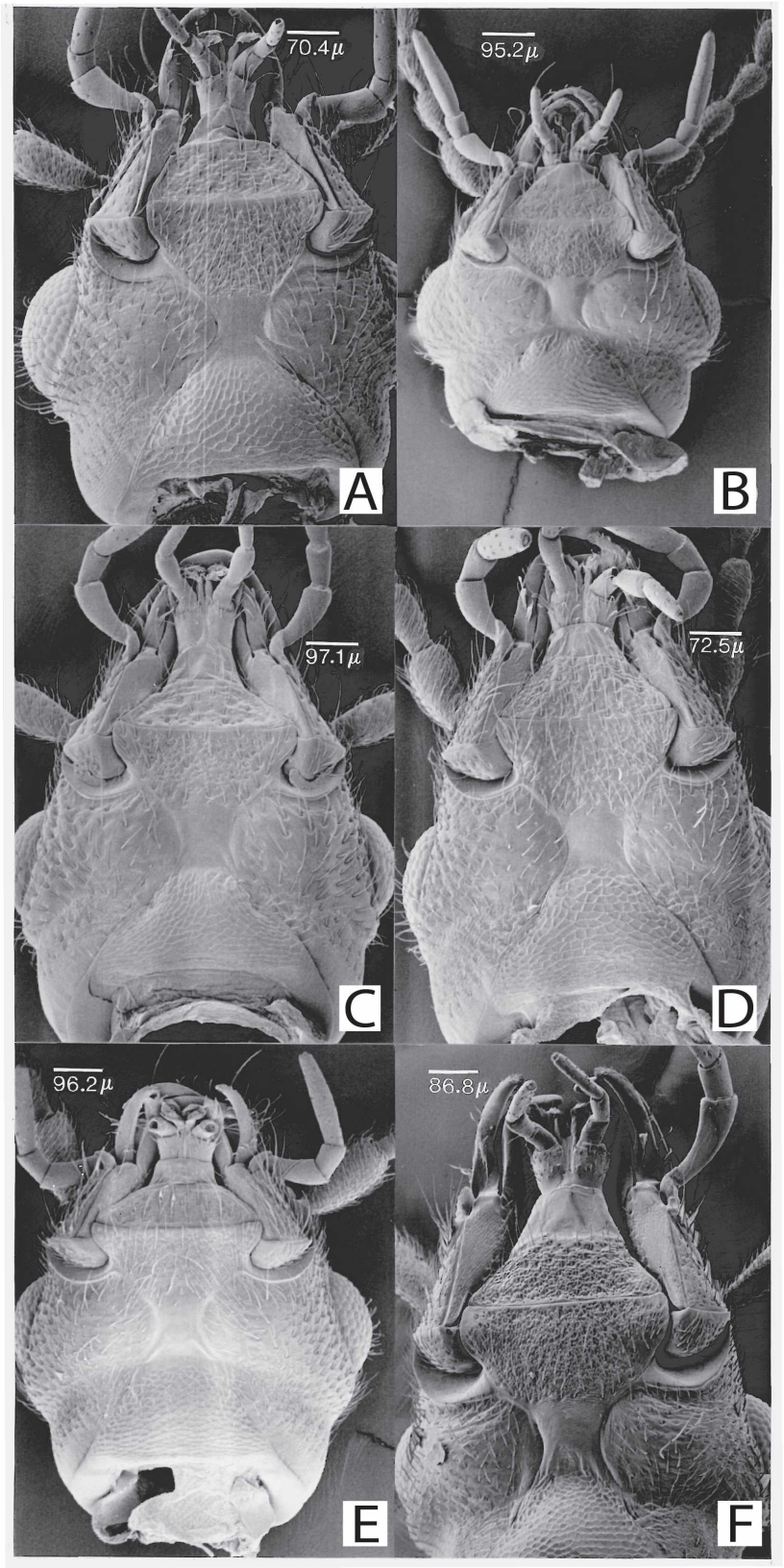

Figure 1.42. Ventral view of head of A) *Unamis* sp. undescribed, B) *Unamis* sp., C) *Phlaeopterus lagrandeuri*, D) *P. houkae*, E) *P. longipennis*, and F) *P. elongatus*.

Table 1.1 Summary of approximate elevation range and habitat of *Phlaeopterus* species based on all known collection events as compiled by J.M. Campbell and specimens databased in this study. Localities are the number of locations > 5 km apart (localities < 5 km apart were counted as one locality) a species has been collected based on the > 3,500 specimens georeferenced in this study. Species are sorted by median elevation. Values in parentheses in the elevation range column represent the elevation range most specimens were collected from for species that usually occur in a notably narrower elevation range between the minimum and maximum elevations.

Species	Elevation (m) midpoint	Elevation range (m)	Habitat	Earliest year collected	Latest year collected	# localities
P. frosti	1025	0-2050 (670-2050)	Snowfields, streams and lakes	1905	1987	30
P. lagrandeuri	1100	0-2,200	Snowfields and streams	1905	2013	41
P. houkae	1130	260-2,000	Streams and snowmelt pools	1935	2013	46
P. fusconiger	1220	240-2,200	Snowfields, sometimes streams	1853	2015	29
P. olympicus	1310	650-1,970 (1,500-1,800)	Snowfields, sometimes streams	1927	1984	7
P. czerskyi	1400	900-1,900	Streams	2006	2016	2
P. bakerensis	1460	1,220-1,700	Snowfields	1931	1979	2
P. castaneus	1550	1,000-2,100	Streams, sometimes snowfields	1885	2014	42
P. obsoletus	1550	1,000-2,100	Streams and waterfalls	1905	1996	28
P. occidentalis	1750	300-3,200	Streams and waterfalls	1905	2015	58
P. hatchi	1760	1,360-2,160	Streams, sometimes snowfields	1905	2012	14
P. cavicollis	1935	670-3,200	Snowfields, sometimes streams	1878	2016	75
P. smetanai	1980	360-3,600	Streams and waterfalls	1905	2006	73
P. loganensis	2100	1,650-2,550 (1,900-2,550)	Streams and waterfalls	1893	2010	23
P. elongatus	2150	1,100-3,200	Snowfields, lakes, and streams	1926	2013	7
P. longipennis	2400	1,800-3,000	Streams	1885	2014	19
P. filicornis	2630	1820-3440 (2800-3440)	Snowfields and streams	1886	1990	20
P. kavanaughi	2830	1,830-3,830	Snowfields	1952	2010	12

Literature Cited

Bernhauer, M., Schubert K., 1910. Pars 19: Staphylinidae I [pp. 1–86]. In: Schenkling, S., (Ed) Coleopterorum Catalogus. Volumen V. Staphylinidae. W. Junk, Berlin, 988 pp.

Blackwelder, R.E., 1952. The generic names of the beetle family Staphylinidae, with an essay on genotypy. *Bulletin of the United States National Museum*, 200: 1–483.

Bousquet, Y., Bouchard, P., Davies, A.E., and Sikes, D.S., 2013. Checklist of Beetles (Coleoptera) of Canada and Alaska. second ed. *ZooKeys* 360: 1–44.

Campbell, J.M., 1978. A revision of the North American Omaliinae (Coleoptera: Staphylinidae) 1. The genera *Haida* Keen, *Pseudohaida* Hatch, and *Eudectoides* new genus. *Memoirs of the Entomological Society of Canada*, 110: 1–20.

Campbell, J.M., 1979. A revision of the North American Omaliinae (Coleoptera: Staphylinidae): 2. The tribe Coryphiini. *Memoirs of the Entomological Society of Canada*, 110: 21–86.

Campbell, J.M., 1982. A revision of the North American Omaliinae (Coleoptera: Staphylinidae): 3. The genus *Acidota* Stephens. *The Canadian Entomologist*, 114 (11): 1003–1029.

Campbell, J.M., 1983. A revision of the North American Omaliinae (Coleoptera: Staphylinidae): 4. The genus *Olophrum* Erichson. *The Canadian Entomologist,* 115: 577–622.

Campbell, J.M., 1984. A revision of the North American Omaliinae (Coleoptera: Staphylinidae): 5. The genera *Arpedzum* Erichson and *Eucnecosum* Reitter. *The Canadian Entomologist,* 11(6): 487–527.

Campbell, J.M., Davies, A., 1991. Checklist of beetles of Canada and Alaska. Agriculture Canada; Canada Communication Group.

Casey, T.L., 1885. New genera and species of Californian Coleoptera. *Bulletin of the California Academy of Sciences*, 7: 281–606.

Casey, T.L., 1886. Descriptive notices of North American Coleoptera I. *Bulletin of the California Academy of Sciences,* 2: 157–264.

Casey, T.L., 1893. Coleopterological Notices V. *Annals of the New York Academy of Sciences*, 7(1): 281–624.

De Queiroz, K., 2007. Species concepts and species delimitation. *Systematic biology*, *56*(6): 879–886.

Elias, S.A., 1985. Paleoenvironmental interpretations of Holocene insect fossil assemblages from four high-altitude sites in the Front Range, Colorado, USA. *Arctic and Alpine Research*, 17(1): 31–48.

Fauvel, A., 1878. Les Staphylinides de l'Amérique du nord. *Bulletin de la Société Linnéenne de Normandie*, 3(2): 167–269.

Gandhi, K.J., Spence, J.R., Langor, D.W. and Morgantini, L.E., 2001. Fire residuals as habitat reserves for epigaeic beetles (Coleoptera: Carabidae and Staphylinidae). *Biological Conservation*, 102(2): 131–141.

Hatch, M.H., 1957. The beetles of the Pacific Northwest. Part II: Staphyliniformia. University of Washington Publications in Biology, 384 pp.

Herman, L.H., 2001. Catalog of the Staphylinidae (Insecta: Coleoptera). 1758 to the end of the second millenium. I. Introduction, history, biogeographical sketches, and Omaliine group. *Bulletin of the American Museum of Natural History*, 265: 1– 650.

International Commission on Zoological Nomenclature, 1999. International Code of Zoological Nomenclature, 4th edition. International Trust for Zoological Nomenclature, London, United Kingdom. Available from: www.nhm.ac.uk/ hosted-sites/iczn/code/.

Hilchie, G.J., 2007. A survey of the beetles (Coleoptera) in Kakwa Wildland Provincial Park. Parks, Conservation, Recreation and Sport Division, Alberta Tourism, Parks, Recreation and Culture.

Jacobson, G.G. 1908. Zhuki Rossii i zapadnoi Evropy. Part 6, A. F. Devriena, St. Petersburg, 79 pp.

Latreille P.A., 1797 Précis des caractères génériques des insectes, disposés dans un ordre naturel. F. Bourdeaux, Brive, 201 pp.

LeConte J.L., 1866. New species of North American Coleoptera. Part 1. Smithsonian Miscellaneous Collections, 167: 1–92.

LeConte, J.L., Horn, G.H. and Henshaw, S., 1883. *Classification of the coleoptera of North America* (Vol. 26, No. 4). Smithsonian Institution.

Maddison, D.R. and Maddison, W.P., 2005. MacClade 4: Analysis of phylogeny and character evolution. Version 4.08 a.

Mäklin, F.G., 1853. [New species and notes]. In: Mannerheim, C.v., Dritter Nachtrag zur Kaefer-Fauna der Nord- Amerikanischen Laender des Russischen Reiches. *Bulletin de la Société Impériale des Naturalistes de Moscou*, 26 (3 & 4): 95–273.

Moore, I., 1966. Notes on the Nearctic Anthophagini with a Key to the Genera (Coleoptera: Staphylinidae). *The Coleopterists Bulletin*, 20(2): 47–56.

Moore, I., Legner, E.F., 1979. An illustrated guide to the genera of the Staphylinidae of America North of Mexico exclusive of the Aleocharinae (Coleoptera). Division of Agricultural Sciences, University of California Priced Publication, 4093, 1–332.

Motschulsky, V. (1853) Nouveautés. *Etudes Entomologiques*, 1: 77–80.

Newton, A.F., Thayer, M.K., Ashe, J.S., Chandler, D.S., 2000. 22. Staphylinidae Latreille, 1802. In: Arnett, R.H. & Thomas, M.C. (Ed.), American Beetles, Vol. 1. Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia, pp. 272–418.

Papp, R.P., 1978. A Nival Aeolian Ecosystem in California. *Arctic and Alpine Research*, 10(1): 117–131.

Scheerpeltz, O., 1933. Staphylinidae VII. In: Schenkling, S. (Ed.), *Coleopterorum Catalogus*, 129: 989–1500.

Shavrin, A.V., 2001. New and little-known species of Omaliinae from the Baikal-Transbaikal area (Coleoptera: Staphylinidae). *Zoosystematica Rossica*, 9: 189-193.

Shavrin, A.V., 2010. Three new species of the genus Lesteva Latreille, 1797 (Coleoptera: Staphylinidae: Omaliinae: Anthophagini) from Uzbekistan, Tadzhikistan and Afghanistan. *Baltic Journal of Coleopterology*, 10(2): 147–152.

Shavrin, A.V., 2014. Review of the genus *Lesteva* Latreille, 1797 (Coleoptera: Staphylinidae: Omaliinae: Anthophagini) of Iran and adjacent territories. *Zootaxa*, 3884(2): 122–140.

Shavrin, A.V., 2015. New data on Himalayan *Lesteva* Latreille, 1797 (Coleoptera: Staphylinidae: Omaliinae) with description of a new species from Nepal. *Zootaxa*, 3973(3): 528.

Shavrin, A.V., Mullen, L.J., 2015. *Phlaeopterus* Motschulsky, 1853 (Coleoptera: Staphylinidae: Omaliinae: Anthophagini)-a new genus for the Palaearctic: new combination. *Zootaxa*, 4028.1: 121–128.

Shavrin, A.V., Shilenkov, V.G. and Anistschenko, A.V., 2007. Two new species and additional records of *Lesteva* Latreille, 1797 from the mountains of South Siberia (Coleoptera: Staphylinidae: Omaliinae: Anthophagini). *Zootaxa*, 1427: 37–47.

Shorthouse, D.P., 2010. SimpleMappr, an online tool to produce publication-quality point maps. [Retrieved from http://www.simplemappr.net. Accessed February 27, 2017]

Wipfler, B., Bai, M., Schoville, S., Dallai, R., Uchifune, T., Machida, R., Cui, Y. and Beutel, R.G., 2014. Ice Crawlers (Grylloblattodea)–the history of the investigation of a highly unusual group of insects. *Journal of Insect Biodiversity*, 2(2): 1–25.

Appendix 1.1. Institutions and respective curators or collections managers from which material was borrowed for this study or studied on location. Abbreviations used here and in text are taken from http://grbio.org/, or from the institutions website or common usage in the literature for collections not featured in the Global Register of Biodiversity list.

AMNH	American Museum of Natural History, New York, New York (Lee H. Herman)
BYU	Monte L. Bean Life Science Museum, Provo, Utah (Shawn M. Clark)
CAS	California Academy of Sciences, San Francisco, California (David H. Kavanaugh, Jere Schweikert)
CAFB	Northern Forestry Centre, Canadian Forestry Service (Gregory Pohl)
CNC	Canadian National Collection of Insects, Ontario, Ottawa (Patrice Bouchard, Anthony Davies)
CSH	Collection of Alexey Shavrin, Daugavpils, Latvia
RBC	Collection of R. Baranowski, Lund, Sweden
CSCA	California State Collection of Arthropods, Sacramento, California (Stephen Gaimari, Andrew Cline, Jacqueline Kishmirian)
DEBU	University of Guelph Insect Collection, Ontario, Canada (Angela Telfer, Jeremy deWaard)
EMEC	Essig Museum of Entomology, Berkeley, California (P. T. Oboyski)
FMNH	Field Museum of Natural History, Chicago, Illinois (Crystal Maier)
INHS	Illinois Natural History Survey, Champaign, Illinois (Michelle Kohler)
ODAC	Oregon Department of Agriculture, Salem, Oregon (James R. Labonte)
OSAC	Oregon State Arthropod Collection, Corvallis, Oregon (Chris J. Marshall)
OSUC	C.A. Triplehorn Insect Collection, Columbus, Ohio (Luciana Musetti)
LSAM	Louisiana State Arthropod Museum, New Orleans, Louisiana (Victoria Moseley Bayless)
MCZ	Museum of Comparative Zoology, Cambridge, Massachusetts (Philip D. Perkins)
MNHN	Museum National d'Histoire Naturelle, Paris, France (Azadeh Taghavian)
MTEC	Montana State Entomology Collection, Bozeman, Montana (Michael A. Ivie)
MZLU	Lund University, Lund, Sweden (Christoffer Fägerström)
NHMO	Natural History Museum, University of Oslo, Norway (Vladimir Gusarov)
NHMUK	Natural History Museum, London, United Kingdom (Max Barclay)
RBINS	Royal Belgian Institute of Natural Sciences, Brussels, Belgium (Yves Samyn)
RBCM	Royal British Columbia Museum, Victoria, British Columbia (Kelly Sendall)
ROM	Royal Ontario Museum, Ontario, Ottawa (Brad Hubley)
SBMNH	Santa Barbara Museum of Natural History (Michael Caterino)
UASM	University of Alberta, E.H. Strickland Entomological Museum, Edmonton, Alberta (F. A. H. Sperling, D. Shpeley)
UAAM	The Arthropod Museum, University of Arkansas, Fayetteville, Arkansas (Jeffrey K. Barnes)

Appendix 1.1, continued.

UAM	University of Alaska Museum Insect Collection, Fairbanks, Alaska (Derek Sikes)
UBCZ	University of British Columbia, Spencer Museum, Vancouver, British Columbia (W. Maddison, Karen Needham)
UCDC	R. M. Bohart Museum of Entomology, Berkeley California (S. L. Heydon)
UCRC	University of California Riverside, Riverside, California (Doug Yanega)
UNHC	University of New Hampshire, Durham, New Hampshire (D. S. Chandler)
USNM	National Museum of Natural History, Washington, DC (Floyd W. Shockley)
WFBM	W.F. Barr Entomological Collection, Moscow, Idaho (Frank W. Merickel)
WIRC	Wisconsin Insect Research Collection, Madison, Wisconsin (Steven Krauth)
WWUIC	Western Washington University Insect Collection, Bellingham, Washington (Merrill A. Peterson)
ZMUC	Zoological Museum, Natural History Museum of Denmark, Copenhagen, Denmark (Alexey Solodovnikov)
ZIN	Zoological Institute, St. Petersburg, Russia (Mark Volkovitsh)

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UNIVERSITY of ALASKA

Logan Mullen <ljmullen2@alaska.edu>

Permission to use CNC / Campbell illustrations in Mullen thesis

Gardner, Nancy <nancy.gardner@agr.gc.ca> Fri, Nov 18, 2016 at 9:24 AM
To: Derek Sikes <dssikes@alaska.edu>, Logan Mullen <ljmullen2@alaska.edu>
Cc: "Savard, Marc" <Marc.Savard@agr.gc.ca>, "Bouchard, Patrice" <Patrice.Bouchard@agr.gc.ca>

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De : Derek Sikes [mailto:dssikes@alaska.edu]
Envoyé : 18 novembre 2016 10:22
À : Gardner, Nancy
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[Quoted text hidden]

Appendix 1.2, continued.

UNIVERSITY of ALASKA

Logan Mullen <ljmullen2@alaska.edu>

P. czerskyi figures

Logan Mullen <ljmullen2@alaska.edu> Wed, Jan 4, 2017 at 11:14 AM
To: Alexey shavrin <ashavrin@hotmail.com>

Hello Alexey,

Hoping this message finds you well.

I am currently finishing up writing the taxonomic revision chapter of my thesis, and wanted to know if I could have your permission to use the Phlaeopterus czerskyi figures from Shavrin and Mullen 2015 in my thesis? I would like to use most of the figures from the paper - the line drawings and the habitus photograph. After I defend my thesis, the figures would ideally also be published in the taxonomic revision of Phlaeopterus, if that is ok with you.

Sincerely,

Logan

--

++++++++++++++++++++++++++++++++++

Logan Mullen, M.S. Student
Department of Biology and Wildlife
University of Alaska Fairbanks

++++++++++++++++++++++++++++++++++

Alexey shavrin <ashavrin@hotmail.com> Wed, Jan 4, 2017 at 12:05 PM
To: Logan Mullen <ljmullen2@alaska.edu>

Hi Logan,

No problem, you can use all these figures for your thesis, papers, etc.

Cheers

Alexey

From: Logan Mullen <ljmullen2@alaska.edu>
Sent: Thursday, January 5, 2017 4:14 AM
To: Alexey shavrin
Subject: P. czerskyi figures

Chapter 2 Morphological and Molecular Phylogeny of the Rove Beetle Genus *Phlaeopterus* Motschulsky, 1853 (Coleoptera: Staphylinidae: Omaliinae: Anthophagini) [2]

2.1 Abstract

The omaliine rove beetle genus *Phlaeopterus* Motschulsky, 1853 contains 18 species, distributed across the northwestern United States, western Canada, Alaska, and Siberia. These beetles are largely confined to the edges of alpine snowfields and streams, habitats that are particularly sensitive to the impacts of climate change. Here, we present the first phylogeny of the genus, using Bayesian and maximum likelihood analyses of morphology and the mitochondrial gene COI. We tested previous taxonomic hypotheses with Bayesian posterior probabilities and found most to be supported, while our *a priori* species-group hypotheses received mixed support. We regard four *Phlaeopterus* species pairs with highly similar COI sequences to be distinct based on morphology, and suggest that *P. castaneus* Casey, 1893 and *P. loganensis* Hatch, 1957 may have hybridized. These findings represent the first modern phylogenetic reconstruction of species-level relationships within the rove beetle subfamily Omaliinae MacLeay, 1825 using both morphology and molecular data. Phylogenetic and taxonomic revisions of other omaliine genera are needed to resolve generic relationships within this beetle group.

[2] Mullen, L.J., Campbell, J.M., Sikes, D.S., In Prep. Morphological and molecular phylogeny of the rove beetle genus *Phlaeopterus* Motschulsky, 1853 (Coleoptera: Staphylinidae: Omaliinae: Anthophagini).

2.2 Introduction

The omaliine rove beetle genus *Phlaeopterus* Motschulsky, 1853, contains 18 species (Chapter 1), distributed across the northwestern United States, Alaska, western Canada, and Eastern Siberia (Fig. 2.1). These small (3–10 mm) brown to black beetles (Fig. 2.2) are largely confined to the edges of permanent or persistent alpine snowfields and cold, cascading streams and waterfalls up to 3,830 meters in elevation (Table 2.1). *Phlaeopterus* adults have been observed foraging on arthropod fallout (mostly flying insects, windblown from lower altitudes and often lethargic or frozen), and mating on the surface of alpine snowfields (Chapter 1). The genus was erected with minimal diagnosis (Motschulsky 1853) based on a single species, *Phlaeopterus fusconiger* Motschulsky, 1853. Additional species were described by Fauvel (1878), Casey (1885, 1886, 1893), Hatch (1957), Shavrin (2001), and Chapter 1. Diagnoses of the genus have been published by Hatch (1957), Moore & Legner (1979), Newton *et al.* (2000), and Shavrin & Mullen (2015). In Chapter 1 I revised the genus, described 8 new species, and synonymized the monotypic genus *Vellica* Casey, 1885 with *Phlaeopterus*. A summary of the taxonomic hypotheses of previous authors, as well as our *a priori* species-group hypotheses, are provided in Table 2.2. Our *a priori* hypotheses were originally conceived by J.M. Campbell based on subjective examination of morphological characters. Phylogenetic relationships within *Phlaeopterus* have never been investigated using modern methods. Here, we present the first Bayesian and maximum likelihood (ML) phylogenetic analyses of *Phlaeopterus*, based on morphological and molecular evidence. Our primary goals were to: 1) estimate the phylogeny of the genus *Phlaeopterus* using Bayesian and ML phylogenetic methods with morphological and

molecular data; and 2) test *Phlaeopterus* generic and species-level hypotheses of published works as well as our *a priori* hypotheses.

2.3 Materials and Methods

2.3.1 Taxon Sampling

All 18 nominal *Phlaeopterus* species were represented in our morphological dataset (Table 2.3), and 17 of these species are represented in our molecular dataset (Table 2.4). Of the 2,635 specimens databased (http://arctos.database.museum/saved/Phlaeopterus) each species was represented by an average of 142.2 specimens (range: 2–325 specimens/species). Wherever possible, multiple exemplars of each *Phlaeopterus* species were included in our molecular dataset, with specimens selected from the widest available geographic range for each species. *Phlaeopterus obsoletus* Campbell in Chapter 1. is missing from our molecular dataset despite repeated attempts to amplify and sequence PCR products. Our outgroup for both the molecular and morphological datasets is composed of 4 *Lesteva* Latreille, 1797 species. *Lesteva* was selected as an outgroup due to our *a priori* hypotheses of close relationship to *Phlaeopterus* based on morphological similarity.

2.3.2 Morphological Data

Our morphological dataset contains 46 characters: 43 external morphological and 3 male genitalic characters (Table 2.3, Appendix 2.1). We coded characters from specimens belonging to, or on loan to, the University of Alaska Museum Insect Collection (Appendix 1.1). We observed characters with a Leica MZ16 stereomicroscope (Leica Microsystems,

Wetzlar, Germany), and coded morphological data in MacClade 4.08 (Maddison and Maddison 2005). We incorporated two tarsal characters (characters 39 and 40 (Appendix 2.1)) from Moore and Legner (1979). Our morphological data matrix and trees are archived at http://purl.org/phylo/treebase/phylows/study/TB2:S21198.

2.3.3 Molecular Data

Our molecular dataset contains 141 sequences of the mitochondrial gene cytochrome c oxidase subunit 1 (COI), representing 17 *Phlaeopterus* species and 4 *Lesteva* species (Table 2.4). We sequenced COI from 108 specimens and added 33 sequences from GenBank and the Barcode of Life Data System (BOLD). Sequences range from 133–658 bp in length. We extracted DNA from whole hind legs using Qiagen DNeasy® extraction kits and following the "Purification of Total DNA from Animal Tissues" protocol in the DNeasy® Blood and Tissue Handbook that came with the extraction kit. We amplified a 658-bp region of COI using the standard COI barcoding forward and reverse primers, LCO-1490 and HCO-2198 respectively (Table 2.5). We used two "mini-barcoding" primer sets, LepF1/MLepF1-Rev (218 bp) and Uni-MinibarF1/Uni-MinibarR1 (133 bp), on extractions that failed to amplify with the standard 658-bp COI primers. We attempted amplification with the LepF1/MLepF1-Rev primer set on all extractions that failed to amplify with the LCO-1490/HCO-2198 primer set. We then attempted amplification with the Uni-MinibarF1/Uni-MinibarR1 primer set on all extractions that failed to amplify with the LepF1/MLepF1-Rev primers. We ran all PCR reactions at 25-µl volume. Typical PCR reaction solution included: 12.5 µl GoTaq Green® Master Mix, 1.0 µl forward primer, 1.0 µl reverse primer, 8.5 µl H_2O, and 2.0 µl template DNA. We used the same thermocycler

protocols for all three primer pairs and followed the methods of Folmer *et al.* (1994) except where noted. Typical thermocycler protocol included a single cycle of 95°C followed by 35 cycles of 95°C for 30 seconds of denaturation, 45°C for one minute of annealing, and 72°C for two minutes of elongation, followed by a single extension of 72°C for 10 minutes.

We viewed sequence data with 4Peaks (Griekspoor and Groothuis 2005) and aligned sequences by eye in MacClade 4.08 and Mesquite 3.04 (Maddison and Maddison 2016). We created consensus sequences from bidirectional reads, aligned by eye, then checked our alignment by translation to amino acids and alignment by amino acid codon position using the "minimize stop codons" option in Mesquite to find the reading frame. The final alignment was free of stop codons and matched a published *Lesteva longoelytrata* (Goeze, 1777) COI sequence (GenBank accession: KM442270.1, Hendrich *et al.* 2015) in both nucleotide and amino acid alignment. Voucher specimens used for DNA extractions can be found in the following insect collections: the University of Alaska Museum (UAM), Canadian National Collection of Insects (CNC), California Academy of Sciences (CAS), Santa Barbara Museum of Natural History (SBMNH), Field Museum of Natural History (FMNH), Smithsonian Museum of Natural History (NMNH), University of Idaho William F. Barr Entomological Museum (WFBM), and Brigham Young University Monte L. Bean Life Science Museum (BYUC). Digital records of all specimens used for molecular work in this study are available through the UAM Arctos database (http://arctos.database.museum/saved/Phlaeopterus). Our molecular data matrix and trees are archived at http://purl.org/phylo/treebase/phylows/study/TB2:S21198. GenBank accession numbers for our sequence data are provided in Table 2.4.

2.3.4 Model Selection

We performed nucleotide substitution model testing for our COI dataset using ModelTest 2.1.10 (Darriba *et al.* 2012) with models considered constrained to those available in MrBayes 3.2.6 (Ronquist *et al.* 2012). The General Time Reversible (Rodriguez *et al.* 1990, Yang 1994) with among-site rate variation (GTR+G) model was the highest scoring under Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC), and the likelihood ratio test. Additionally, we used PartitionFinder (Lanfear *et al.* 2012) to chose a partition scheme and model of sequence evolution using the BIC. This found partitioning the COI dataset by codon position (1^{st}, 2^{nd}, and 3^{rd}) with the GTR+I+G for each to be optimal, although the -lnL scores of the two highest scoring models, the GTR+I+G model (-lnL = 3737.36347) and the GTR+G model (-lnL = 3737.35508), were nearly identical. Given that Bayesian methods have been shown to be more sensitive to model underspecification than overspecification (Huelsenbeck and Rannala 2004), we used the more complex model, GTR+I+G partitioned by codon position, in all analyses.

We used Bayes Factors factors (Kass and Raftery 1995) to determine if gamma correction for among-character rate heterogeneity was warranted for the Mkv model (Lewis 2001) used for the morphological data. To compare the performance of the two possible model plus parameter combinations (*e.g.,* Mkv with or without gamma distribution), we compared the harmonic mean of the marginalized likelihood scores of two independent Metropolis-Coupled Markov Chain Monte Carlo (MCMCMC) chains. We ran each analysis of 4 chains for 10,000,000 steps using MrBayes 3.2.6 with default priors. We sampled every 1,000 steps resulting in 10,000 trees sampled. We discarded the first 25% (2,500 trees) as burn-in resulting in 7,500 post burn-in trees. The absolute difference

between these two harmonic means was <1.0, suggesting that adding gamma distribution to the Mkv model did not improve the fit of this model to the data (Kass and Raftery 1995), so the Mkv model without gamma distribution was used. Bayesian analysis has been shown to be more accurate than parsimony analysis for morphological datasets with heterogeneous substitution rates (Wright and Hillis 2014), which are likely for most real-world datasets. For this reason, we did not conduct parsimony analysis in this study.

2.3.5 Bayesian Phylogenetic Analyses

We analyzed multiple permutations of the morphological and molecular datasets with Bayesian methods. We analyzed the COI dataset both independently and concatenated with the morphological data. We tested the monophyly of species using a full dataset of 141 COI sequences. To reduce computational complexity, we reduced the dataset to a single exemplar sequence per species (henceforth "COI pruned"), using the longest sequence available for each species. We analyzed the COI pruned dataset alone as well as concatenated with the morphological dataset. We incorporated the species lacking molecular data (*P. obsoletus*) into the concatenated analysis by using morphological data and missing data (-) for each molecular character for this taxon. We compared results of all permutations (COI only, morphology only, concatenated COI+morphology, and COI pruned vs. COI full) for differences in topology and support.

We performed all Bayesian analyses using MrBayes 3.2.6. Each analysis was rooted with *Lesteva pubescens*. We ran each analysis using 4 chains for 10,000,000 steps with default priors and sampled every 1,000 generations resulting in 10,000 trees sampled. We

discarded the first 25% (2,500 trees), resulting in 7,500 post burn-in trees. To determine if stationarity had been reached, we evaluated all MCMCMC chains in Tracer v1.6 (Rambaut *et al.* 2014) using the following criteria: 1) split frequencies less than or equal to 0.01, 2) effective sample size (ESS) greater than 100 for all parameters, 3) visual inspection of trace file for stability of –lnL values after the burn-in period. Furthermore, we checked that posterior probability (PP) support values and topology did not vary significantly between two or more replicates of each analysis. All runs conducted in this study reached stationarity based on these criteria.

2.3.6 Maximum Likelihood Phylogenetic Analyses

We performed maximum likelihood (ML) analyses on the pruned COI+morphology dataset only using Garli 2.01 (Zwickl 2006) on the CIPRES Science Gateway v3.3 (Miller *et al.* 2010). The four *Lesteva* species were specified as outgroups. We evaluated a stepwise-addition starting tree with 50 attachment branches for each taxon, with no starting topology specified. We combined ten independent runs of 50 bootstrap (BS) repetitions each into a single treefile. We assembled a 50% majority rule consensus tree of the resulting 500 BS replicates using PAUP 4.0 (Swofford 2003).

2.3.7 Hypothesis Testing

We tested the monophyly of taxonomic hypotheses of previous researchers, as well as our *a priori* taxonomic groupings using PP support values obtained from Bayesian analyses (Table 2.6). Taxon relationships that did not occur in any of the sampled trees in

an MCMCMC run were assumed to have a PP of <1/number of trees sampled (Miller *et al.* 2002). In our analyses, such clades would have a PP <1/7,500 trees sampled, or PP <0.0001. We tested the monophyly of *Phlaeopterus* species using the full 141-sequence COI dataset (Table 2.4).

2.4 Results

2.4.1 Sequence Statistics

Our COI alignment is 658 bp long and comprised 141 sequences. Base composition is as follows: A=29.72% C=17.17% G=16.47% T=36.65% (Table 2.7). These values are within the range typically reported for insect mitochondrial DNA (Dowton and Austin 1997). Our full 141-sequence COI dataset contains 195 parsimony-informative sites, with over 83% (n=163) found in the 3rd codon position (Table 2.7). The 25 "short" 133–241 bp COI sequences, those sequenced with the Uni-MinibarF1/Uni-MinibarR1 or LepF1/MLepF1-Rev primer pairs, contain 44 parsimony informative sites (Table 2.7). The Chi-square test of homogeneity of base frequencies across taxa as implemented in PAUP* 4.0 resulted in a Chi-square value = 139.6243 (df = 423) with a p-value = 1.0, suggesting that nucleotide frequencies across taxa were stationary. However, this test assumes independence of sequences, which is likely violated by the shared evolutionary history and uneven taxon sampling of our dataset.

Uncorrected p-distances within and among *Phlaeopterus* species COI sequences are summarized in Figure 2.7. *Phlaeopterus castaneus* Casey, 1893 has a maximum within-species difference of 3.78% and a minimum among-species difference of 0% with *P.*

loganensis. Similarly, *P. cavicollis* (Fauvel, 1878) has a maximum within-species difference of 1.13% and a minimum among-species difference of 0.19% with *P. occidentalis* Campbell in Chapter 1. *Phlaeopterus loganensis* Hatch, 1957 (Fig. 2.7) has a maximum within-species difference of 0.38% and a minimum among-species difference of 0% with *P. castaneus.* All other congeneric among-species COI sequence comparisons fall above 2% and all other within-species comparisons fall below 2%. However, *P. obsoletus* Campbell in Chapter 1., the species missing sequence data, and those species represented only by sequences <300 bp in length or a single 658 bp sequence (*P. czerskyi* (Shavrin, 2001), *P. hatchi* Campbell in Chapter 1., *P. frosti* Hatch, 1957, *P. bakerensis* Campbell in Chapter 1., *P. occidentalis, P. filicornis* (Casey, 1893), and *P. olympicus* Campbell in Chapter 1.) were excluded from this analysis. We excluded species represented by a single 658 bp sequence because they would lack within-species difference values. We excluded sequences <300 bp in length because comparing the percent differences between two 658 bp sequences to the percent difference between a 658 bp and a 133 bp sequence would be inaccurate.

We tested for saturation in our COI dataset using DAMBE6.4.40 (Xia *et al*. 2003, Xia and Lemey 2009) and found that there was little substitution saturation. The I_{ss} value of the 1st and 2nd codon positions = 0.612, which is significantly less than the $I_{ss.c}$ value = 0.7159 ($P < 0.0001$, two tailed *t* test). The I_{ss} value of the 3rd codon position = 0.5552, which is significantly less than the $I_{ss.c}$ value = 0.6920 ($P = 0.0001$, two-tailed *t*-test).

2.4.2 Bayesian and Maximum Likelihood Phylogenetic Analyses

The most inclusive phylogeny of *Phlaeopterus* presented in this study is the pruned combined COI+morphology phylogeny, with the species missing molecular data (*P.*

obsoletus) analyzed using morphological data only. A 50% majority rule consensus tree of this analysis with both Bayesian and ML BS support values is shown in Figure 2.3. This tree is well resolved except for two polytomies in the genus *Phlaeopterus*. Most branches have ML BS support values similar to or lower than Bayesian PP support values, but the branch supporting *P. kavanaughi* Campbell in Chapter 1. + *P. castaneus* has higher ML support (BS = 100) than Bayesian support (PP = 0.53).

2.4.2.1 Molecular Phylogeny

A 50% majority rule consensus tree of the pruned COI dataset is shown in Figure 2.4. This tree is less well resolved than the combined COI+morphology phylogeny (Fig. 2.3) and has a 5-branch polytomy in the "backbone" of the genus *Phlaeopterus*. This phylogeny differs from the combined COI+morphology phylogeny in the placement of *P. lagrandeuri* Hatch, 1957 and *P. elongatus* Campbell in Chapter 1 as sister species with high support (PP = 0.81), and in the placement of *P. bakerensis* in a trichotomy with *P. longipennis* and *P. olympicus*, although with negligible support (PP = 0.54). A 50% majority rule consensus tree of 7,500 post burn-in trees of the full 141 sequence COI dataset (Fig. 2.5) is, not surprisingly, very similar in topology and support values to the pruned COI phylogeny (Fig. 2.4). The full COI phylogeny supports the monophyly of most *Phlaeopterus* species, but four species pairs form intermixed clades (i.e., the individual species are not monophyletic): 1) *P. fusconiger* + *P. frosti*, 2) *P. cavicollis* + *P. occidentalis,* 3) *P. castaneus* + *P. loganensis*, and 4) *P. filicornis* + *P. hatchi*.

2.4.2.2 Morphological Phylogeny

The 50% majority rule consensus tree of the morphology dataset (Fig. 2.6) is less well resolved than the combined analysis and contains two polytomies of 5 and 7 branches, respectively. This tree agrees with our *a priori* genus and species-group hypotheses with the exception of the *fusconiger* species group which is unresolved in a polytomy. The *cavicollis, filicornis*, and *longipennis* species groups are well supported with PP = 0.98, 0.99, and 0.93 respectively.

2.4.2.3 Hypothesis Testing

A summary of Bayesian PP support for taxonomic hypotheses of *Phlaeopterus* in the COI+morphology (Fig. 2.3), COI-only (Fig. 2.4), and morphology-only (Fig. 2.6) phylogenies is given in Table 2.6. Except for those of Mäklin (1853) and Shavrin (2001), all published testable (not monotypic) taxonomic hypotheses were well supported (PP > 0.90) by all three analyses. Our *a priori* species-group hypotheses have mixed support in the morphology-only (Fig. 2.6) and COI+morphology (Fig. 2.3) phylogenies but are all rejected with PP < 0.0001 in the COI-only phylogeny (Fig. 2.4). Our *filicornis* species-group hypothesis is supported with PP = 0.99 in the morphology-only (Fig. 2.6) and COI+morphology (Fig. 2.3) phylogenies, but is rejected with PP < 0.0001 in the COI-only phylogeny (Fig. 2.4). Support for parts of those groupings is found in the COI-only phylogeny (Fig. 2.5), however, which shows close relationships of *P. castaneus* and *P. kavanaughi* (our *a priori castaneus* species group); *P. fusconiger* and *P. frosti* (part of our *a priori fusconiger* species group); and *P. filicornis* and *P. hatchi* (part of our *a priori filicornis* species group).

2.5 Discussion

Here we present the first Bayesian and ML phylogeny of the genus *Phlaeopterus*, using both morphology and molecular (COI) data. These analyses were used to test all previous taxonomic hypotheses of the genus and our *a priori* hypotheses (Table 2.6), as well as the monophyly of *Phlaeopterus* species (Figs. 2.5, 2.7). We found strong support for the synonymy of *Vellica* under *Phlaeopterus* (Figs. 2.5–2.7, Table 2.6) in Chapter 1. (in prep.). This is in agreement with Newton *et al.* (2000) who suggested that *Vellica* was likely not distinct from *Phlaeopterus*. The combined COI+morphology phylogeny (Fig. 2.3) is more comprehensive than the COI-only (Fig. 2.4) or morphology-only (Fig. 2.6) phylogenies because it incorporates evidence from both morphology, which is encoded by the nuclear genome, and mitochondrial DNA data, and includes two species lacking molecular data that are missing from the COI-only phylogeny (*P. smetanai* Campbell in Chapter 1. and *P. obsoletus*). However, it should be noted that concatenation has drawn criticism because it can fail to account for varying histories of genes and can produce strongly supported but incorrect trees (Kubatko and Degnan 2007). In cases of conflict between morphology (Fig. 2.6) and COI (Fig. 2.4), the COI+morphology phylogeny recovers a topology more similar to the morphology-only phylogeny (Fig. 2.6). Testing the monophyly of *Phlaeopterus* would benefit from taxon sampling beyond what was performed in this study. However, comprehensive outgroup sampling to test the monophyly of *Phlaeopterus* would be challenging because the tribe Anthophagini is likely not monophyletic (Newton *et al.* 2000). The known morphological characters to delimit *Phlaeopterus* from *Lesteva*, the outgroup used in this study, include characters 3–6, 9–15, 18, 20, 21, 33, 34, 36, and 38–40 (Appendix 2.1). These characters were only coded for four of the ca. 109 described species

of *Lesteva* (Herman 2001, Shavrin 2014), and additional species are still being described at a high rate (*e.g.* Shavrin *et al.* 2007, Shavrin 2010, 2014, 2015).

2.5.1 Conflict in Bayesian Analyses of Morphology vs. Molecules

Differences in topology, resolution, and branch support were observed between morphology-only (Fig. 2.6), COI-only (Fig. 2.4), and combined COI+morphology (Fig. 2.3) analyses in this study. The mitochondrial genome has an effective population size that is ¼ that of the somatic portions of the nuclear genome in diploid organisms, resulting in much shorter coalescence times (Wiens and Penkrot 2002). A large polytomy in the "backbone" of the COI phylogeny (Fig. 2.4) suggests that saturation may be confounding the phylogenetic signal of this dataset at deeper nodes. However, the index of substitution saturation test we performed using DAMBE6 found that little substitution saturation had occurred in our COI dataset. Morphological data provides a useful contrast to mtDNA, as each morphological character is coded by many nuclear markers, and therefore may approximate their phylogenetic signal. Clearly, each type of data has strengths and limitations, and the strengths of each can complement the limitations of others. Hillis and Wiens (2000) and Wiens (2004) provide excellent summaries of the arguments for the use of both morphology and molecular data in phylogenetic analysis. For these reasons we have emphasized comparison of morphological and molecular phylogenies in this study.

2.5.2 Identical or Highly Similar COI Sequences in Morphologically Distinct Species Pairs

Four *Phlaeopterus* species pairs form intermixed clades in the full COI phylogeny (Fig. 2.5). Two of these pairs, *P. loganensis* + *P. castaneus* and *P. cavicollis* + *P. occidentalis,* were included in an analysis of uncorrected within- and among-species p-distances (Fig. 2.7) and have uncorrected among-species p-distances of less than 2%. Specimens of *P. castaneus* (Table 2.4, UAMObs:Ento:232749) and *P. loganensis* (Table 2.4, UAMObs:Ento:232748) have identical COI haplotypes. Further investigation suggests that human error is unlikely to be the explanation for these identical sequences. The two specimens were collected from different localities and sequenced at different times, and the identifications of these two specimens has been confirmed by Anthony Davies of the Canadian National Collection of Insects and the first author. Furthermore, these results are corroborated by additional pairs of *P. castaneus* and *P. loganensis* sequences with less than 1% divergence. The known distribution of *P. loganensis* is entirely within that of *P. castaneus*. Morphologically, these two species are quite distinct: *P. loganensis* has the autapomorphy of the elytra being prolonged at the suture (Fig. 2.8a) whereas *P. castaneus* has broadly rounded elytral margins, which is the state typical of *Phlaeopterus* and related taxa (Figs. 2.8b, 2.8c). Interestingly, *P. castaneus* forms two distinct clades in the full COI phylogeny (Fig. 2.5). Only one of these *P. castaneus* clades is intermixed with *P. loganensis* COI sequences, with this clade containing only sequences from the Rocky Mountains, and the other P. *castaneus* clade containing only sequences from the Cascade Mountains. This pattern suggests that *P. castaneus* has recently hybridized with *P. loganensis* in the Rocky Mountains (*P. loganensis* is only known from the Rocky Mountains and Selkirk Mountains)

and that the *P. loganensis* haplotype replaced the P. *castaneus* haplotype in the Rocky Mountains but not in the Cascade Range. Future research could test this hypothesis by sampling multiple unlinked nuclear loci from both species in the Rocky Mountains and from *P. castaneus* in the Cascade Range. Nuclear loci are less likely to be introgressed than mitochondrial DNA (Funk and Omland 2003) and could therefore be used to determine if introgression of mitochondrial DNA has occurred.

Three additional species pairs, *P. cavicollis* + *P. occidentalis*, *P. fusconiger* + *P. frosti*, and *P. filicornis* + *P. hatchi*, are unresolved in the full COI phylogeny (Fig. 2.5). Each pair are sister species in the morphology-only phylogeny (Fig. 2.6) and can be distinguished by morphological characters (Table 2.3). *Phlaeopterus cavicollis* and *P. occidentalis* can be distinguished by the pronotal lateral margin being broadly and subequally explanate anterior and posterior to the lateral foveae in *P. cavicollis* (Fig. 2.9a) and broadly explanate posterior but not anterior to the lateral foveae in *P. occidentalis* (Fig. 2.9b). *Phlaeopterus fusconiger* and *P. frosti* can be distinguished by the length of the glabrous apex of the mesotibia (Fig. 2.10) and the length and sclerotization of the internal sac of the aedeagus (Fig. 2.11). *Phlaeopterus filicornis* and *P. hatchi* differ in the internal sac of the aedeagus (Fig. 2.11), the sinuate apical margins of the median lobe of the aedeagus, and the apex of the elytra, which is sexually dimorphic in *P. filicornis* but not *P. hatchi* (Fig. 2.8). Missing data may account for the lack of resolution within all three pairs of species, as all *P. frosti* sequences in our dataset are <170 bp long, the two *P. occidentalis* sequences in our dataset are 218 bp in length, and the three *P. filicornis* sequences and single *P. hatchi* sequence in our dataset are 218 bp in length. These results may also be due to lineage sorting (Maddison 1997) or infections of the bacterium *Wolbachia* (Whitworth *et al.* 2007). Studies

of sequence divergence within various insect groups have reported large variation of within- and among-species distances (Cognato 2006, Trewick 2008) and high rates of non-monophyly of animal species (Funk and Omland 2003). These unresolved species pairs could be improved with additional mitochondrial and nuclear loci, which is beyond the scope of this study. Therefore, I have chosen the morphological phylogenetic signal, which indirectly represents the nuclear genome, over COI in these cases. This decision is represented in the COI+morphology phylogeny (Fig. 2.3) as well as the morphological phylogeny (Fig. 2.6).

2.5.3 Conflict between Bayesian and Maximum Likelihood Methods

Maximum Likelihood phylogenetic analyses tend to be more conservative than Bayesian analyses, with Bayesian methods more prone to supporting true relationships but less prone to rejecting false relationships than ML methods (Erixon *et al.* 2003, Douady *et al.* 2003). ML BS support values in this study are similar to or lower than Bayesian PP support values in the combined COI+morphology phylogeny (Fig. 2.3), except for the branch supporting *P. kavanaughi* + *P. castaneus*, which has higher ML support (BS = 100) than Bayesian support (PP = 0.53). Conflicting phylogenetic signal between our morphological and molecular datasets may be a confounding factor in the placement of *P. castaneus*, *P. kavanaughi*, and *P. loganensis* in our Bayesian and maximum likelihood analyses. *Phlaeopterus castaneus* and *P. kavanaughi* are recovered as sister species in the morphology-only phylogeny (Fig. 2.6), but *P. castaneus* and *P. loganensis* are recovered as sister species in the pruned COI-only phylogeny (Fig. 2.4). In all three analyses, the clade *P. castaneus* + *P. kavanaughi* + *P. loganensis* is recovered (Figs. 2.3–2.4, 2.6).

2.5.4 Future Directions for Anthophagine Phylogenetics

The phylogeny of the tribe Anthophagini, to which *Phlaeopterus* belongs, is largely unknown. The tribe contains 27 North American genera, of which only seven have been taxonomically revised (Campbell 1978, 1982, 1983, and 1984). Furthermore, Anthophagini has been referred to as a taxonomic dumping ground, as it lacks synapomorphies for all included genera and is likely not monophyletic (Newton *et al.* 2000). Here, we present the first phylogeny of an anthophagine genus, and furthermore the first modern phylogenetic reconstruction of species-level relationships within the rove beetle subfamily Omaliinae MacLeay, 1825 using both morphology and molecular data. It is our hope that the coming years will see the production of much needed phylogenetic and taxonomic revisions of other anthophagine genera, resolving generic and sub-generic relationships within this fascinating and poorly studied beetle group.

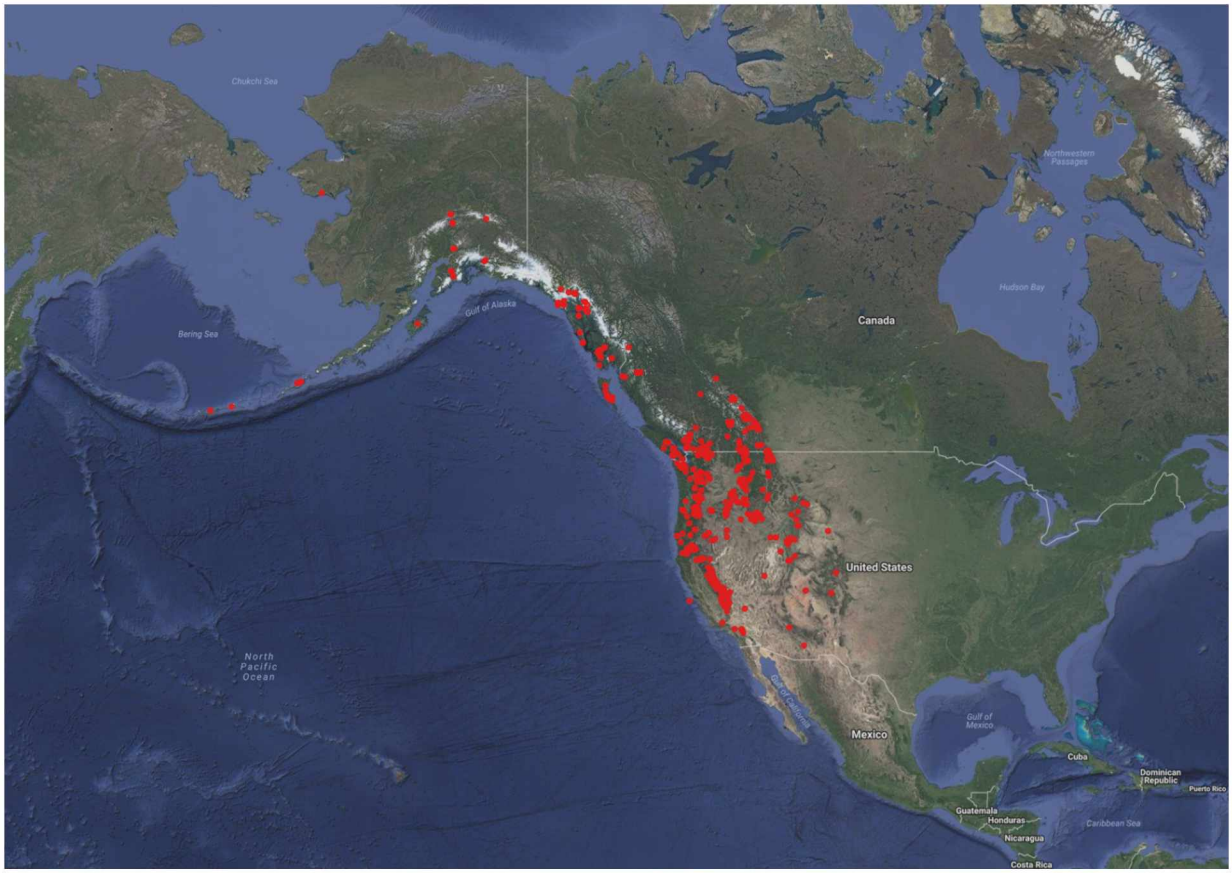

Figure 2.1. North American distribution of the genus *Phlaeopterus* based on over 3,500 georeferenced museum records for the genus in the Arctos database and visualized with BerkeleyMapper. Not pictured is the locality of the single Asian *Phlaeopterus* species, *Phlaeopterus czerskyi*, known only from the Khamar-Daban Mountains of East Siberia (51º46' N, 103º95' E).

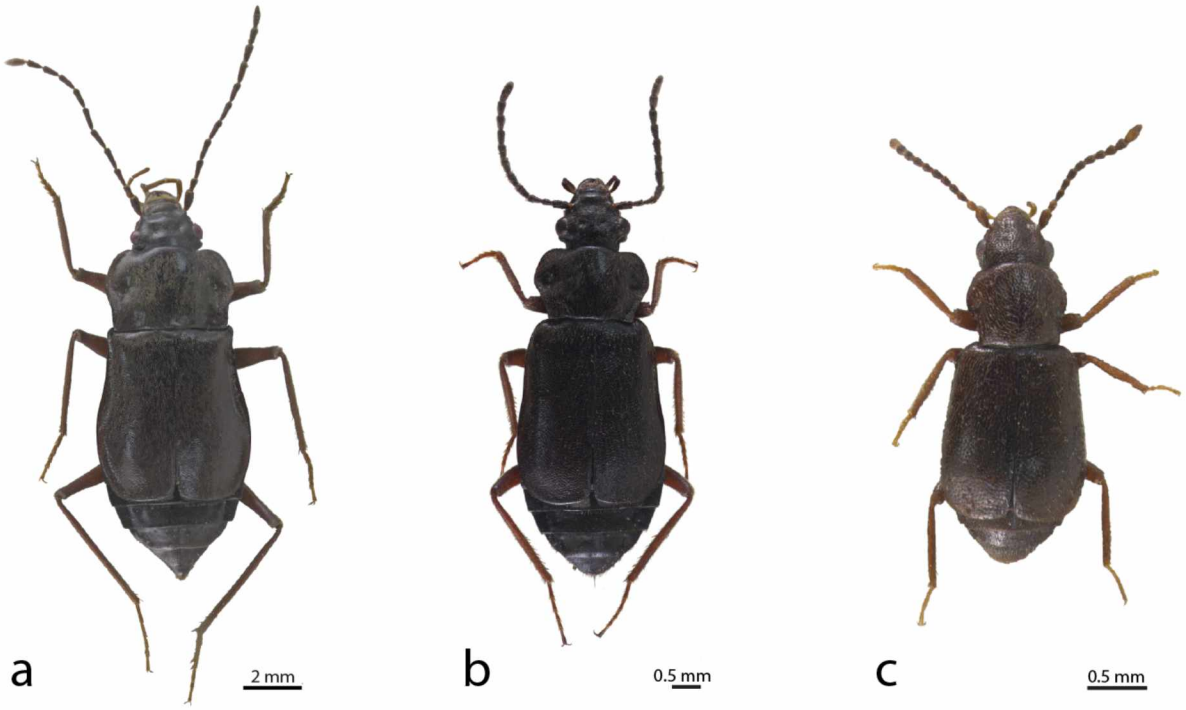

Figure 2.2. Habitus photos of A) *Phlaeopterus bakerensis*, the largest *Phlaeopterus* species: length = ~10 mm, B) *Phlaeopterus occidentalis* a medium sized species: length = ~7mm, and C) *Phlaeopterus obsoletus*, the smallest *Phlaeopterus* species: length = ~3 mm.

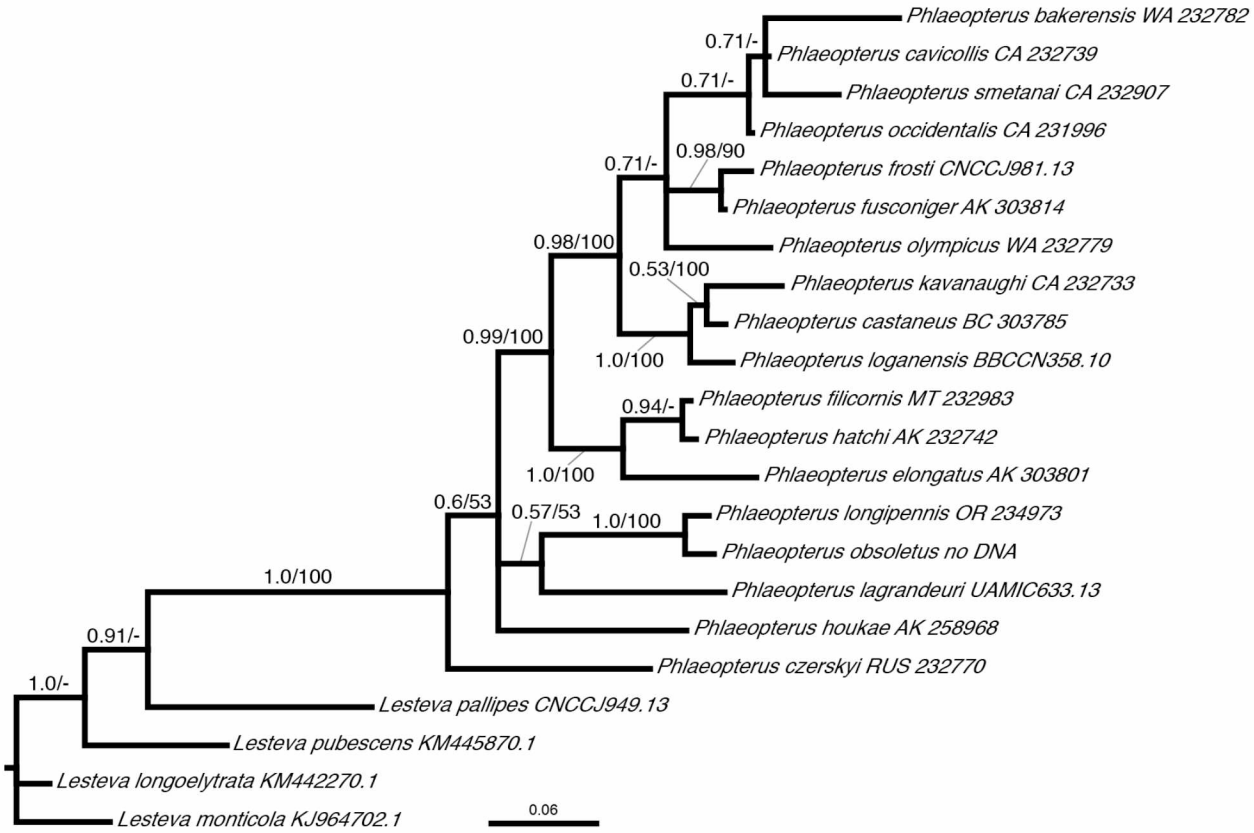

Figure 2.3. Bayesian analysis of 46 morphological characters and 658–133 bp of COI with Bayesian posterior probability support values and maximum likelihood bootstrap support values above each branch with 18 *Phlaeopterus* species and 4 *Lesteva* outgroup species. Topology is a Bayesian 50% majority rule consensus phylogram of 7,500 post burn-in trees of a concatenated analysis using the Mkv model for the morphology partition and the GTR+G model for each codon position partition of the COI dataset in MrBayes 3.2.0 software. Bootstrap values are derived from a 500 bootstrap replicate maximum likelihood concatenated analysis using Garli 2.01 software on the same datasets and with the same models and partitions. Clades that did not occur in a 50% majority rule consensus tree of the 500 bootstrap replicates are indicated with a "-" .

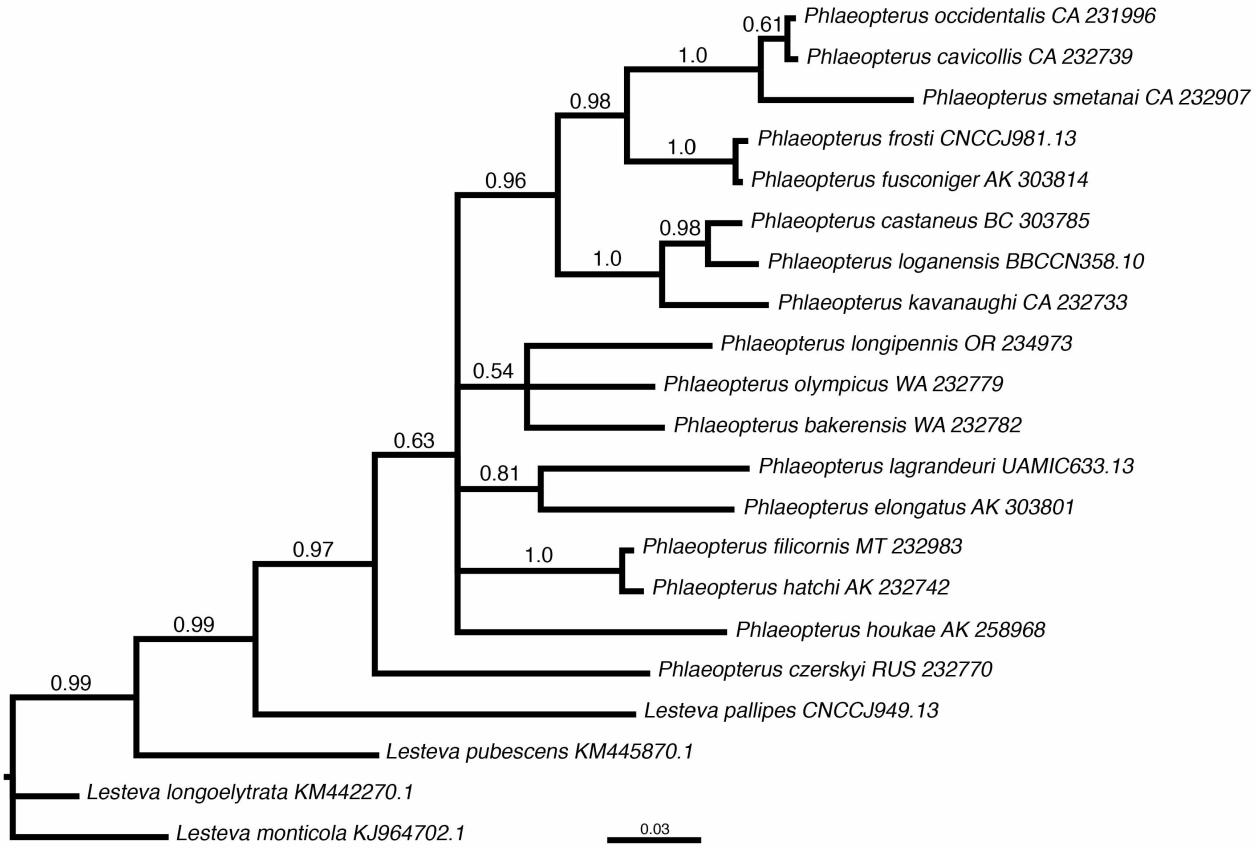

Figure 2.4. Bayesian analysis of 133–658 bp of the mitochondrial gene COI with Bayesian posterior probability support values above each branch with 15 *Phlaeopterus* species and 4 *Lesteva* outgroup species. 50% majority rule consensus phylogram of 7,500 post burn-in trees using the GTR+G model for each codon position in MrBayes 3.2.0 software. The full COI dataset (Fig. 2.5) was pruned to a single exemplar sequence for each species, with exemplars selected by the criteria of sequence length and completeness.

Figure 2.5 (see caption on page 171)

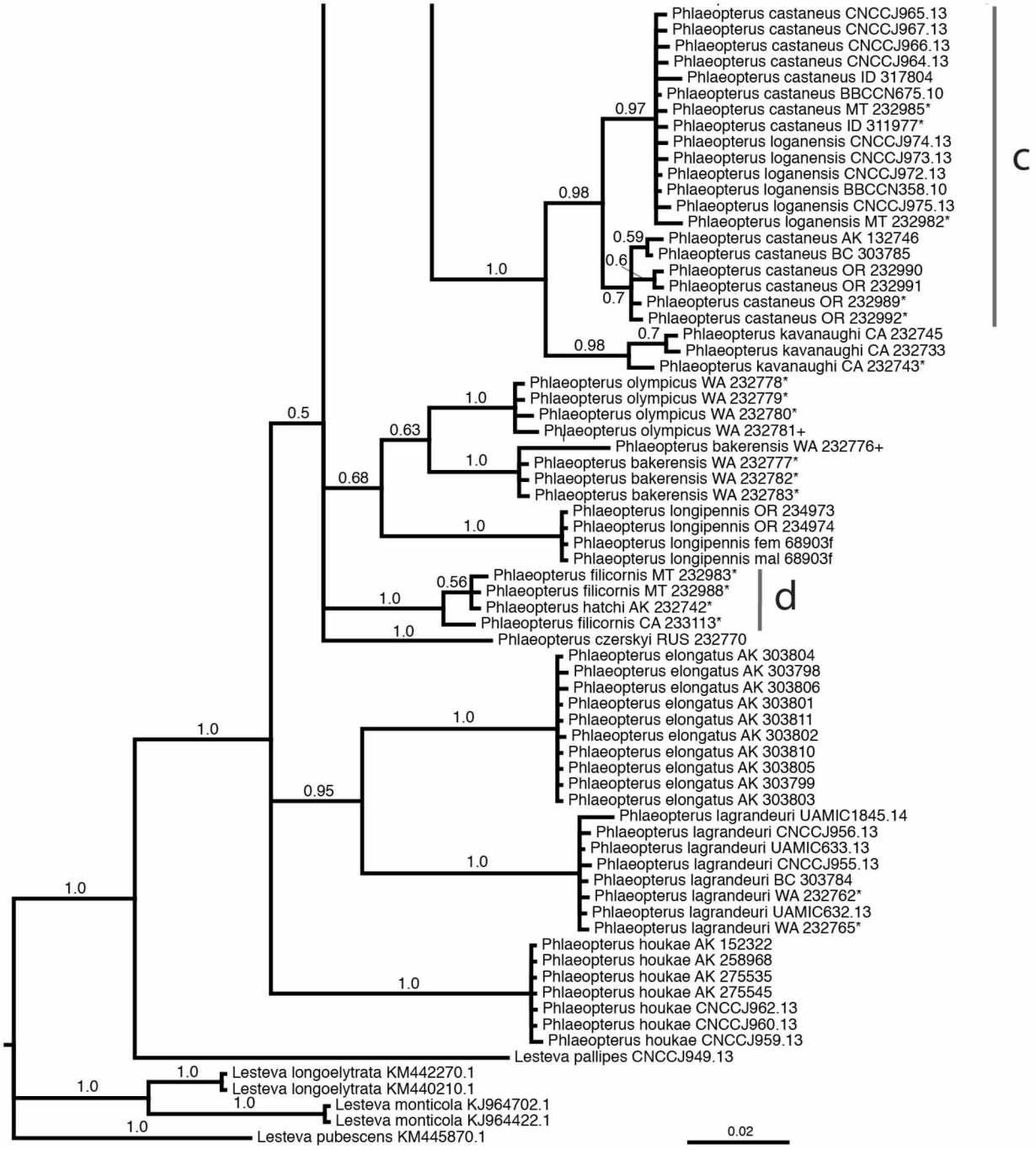

Figure 2.5 continued.

Figure 2.5. Bayesian analysis of 141 sequences, 133–658 bp in length, of the mitochondrial gene COI with Bayesian posterior probability support values above each branch with 15 *Phlaeopterus* species and 4 *Lesteva* outgroup species. 50% majority rule consensus phylogram of 7,500 post burn-in trees using the GTR+G model in MrBayes 3.2.0 software. The full COI dataset was used here to test the monophyly of *Phlaeopterus* species. Four species pairs formed intermixed clades and are indicated: a. *P. fusconiger* + *P. frosti*, b. *P. cavicollis* + *P. occidentalis*, c. *P. castaneus* + P. *loganensis*, and d. *P. filicornis* + *P. hatchi*. Short sequences are marked as follows: "*"= 218 bp in length, "+"= 133 bp in length.

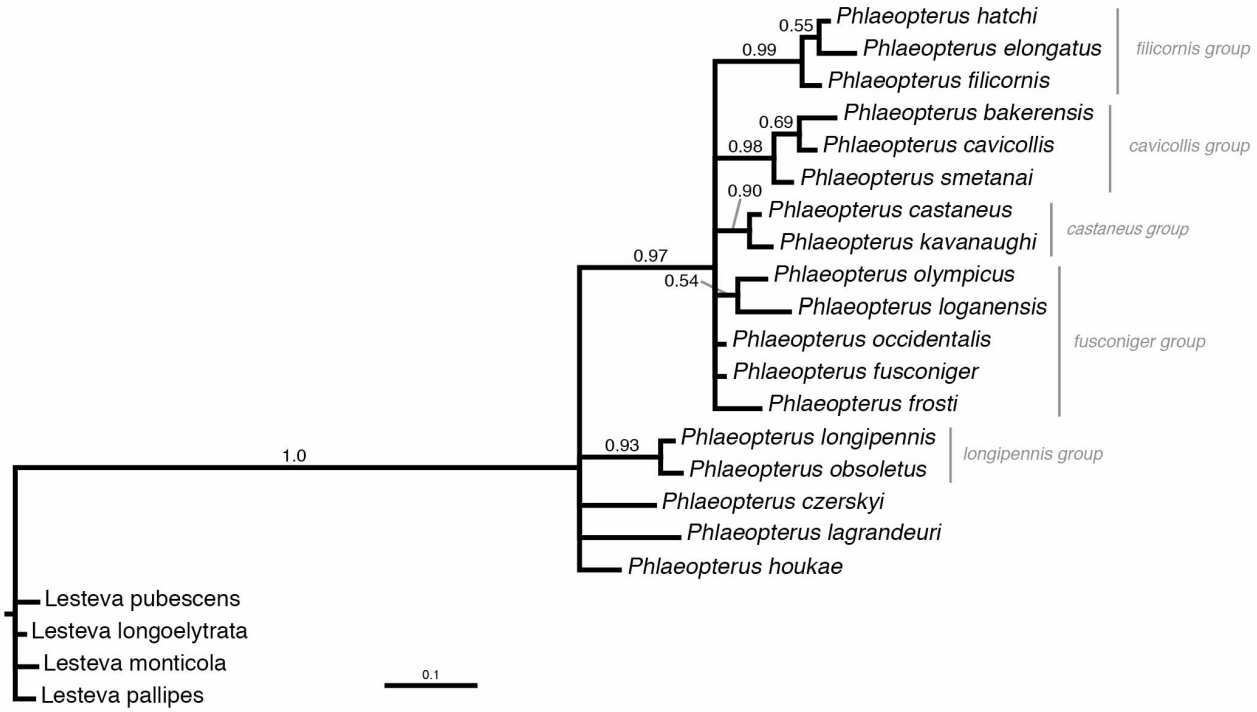

Figure 2.6. Bayesian analysis of 46 morphological characters with Bayesian posterior probability support values above each branch with 18 *Phlaeopterus* species and 4 *Lesteva* outgroup species. 50% majority rule consensus phylogram of 7,500 post burn-in trees using the Mkv model in MrBayes 3.2.0 software. Our *a priori* informal species-group hypotheses are shown in grey.

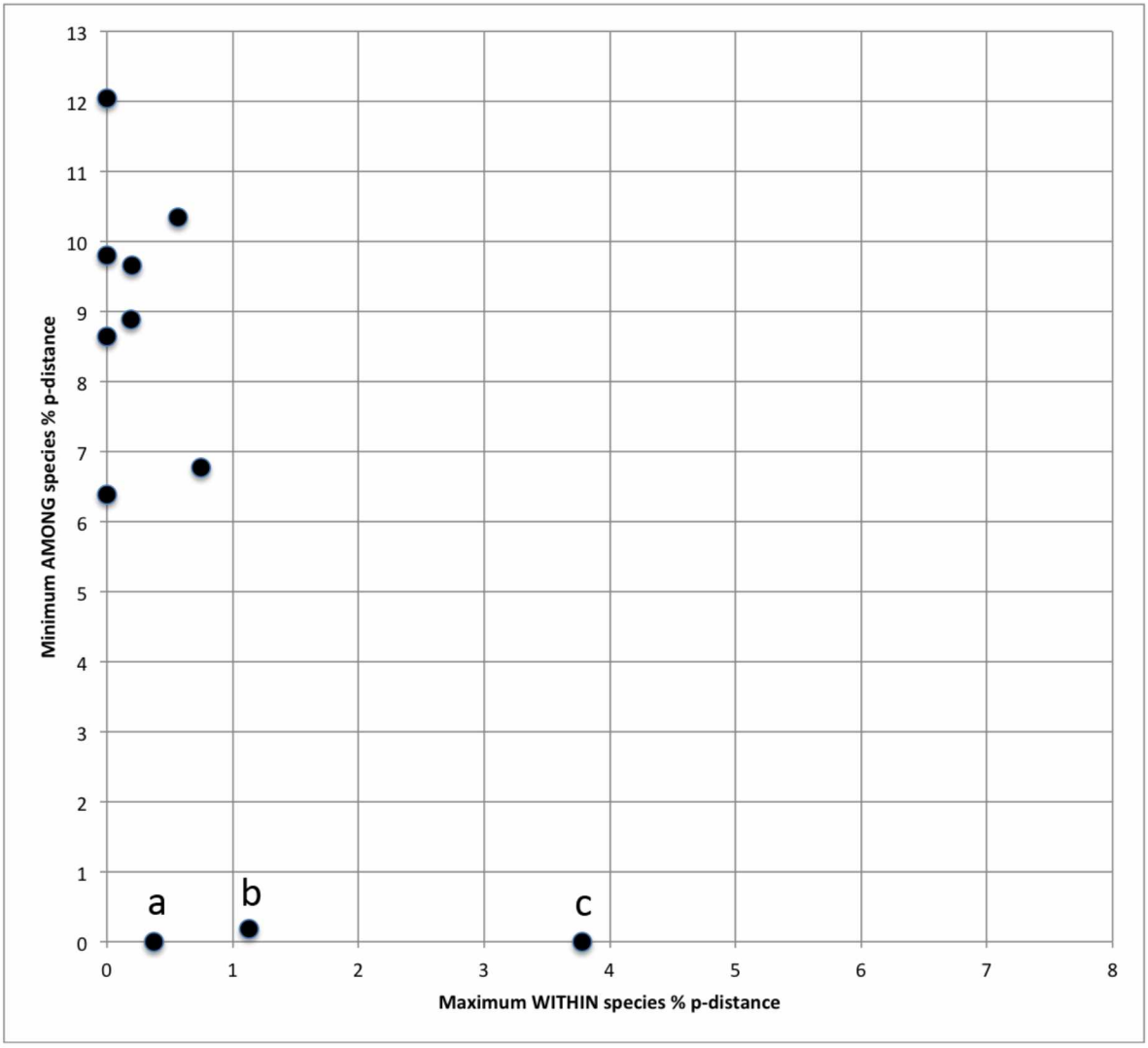

Figure 2.7. Maximum within-species p-distances versus minimum among-congeneric species p-distances for the COI dataset (Table 2.4) for a total of 4,851 sequence-pair comparisons. Sequences with > 50% of base pairs missing (< 300 bp) were excluded. Excluded sequences included all those amplified with the LepF1/MLepF1-Rev (211 bp target length) and Uni-MinibarF1/Uni-MinibarR1 (133-bp target length) primer pairs. Note the three species with minimum among species % p-distance below 2%: a. *Phlaeopterus loganensis*, b. *Phlaeopterus cavicollis*, and c. *Phlaeopterus castaneus*. *Phlaeopterus occidentalis*, *Phlaeopterus filicornis*, and *Phlaeopterus hatchi* would likely also fall below 2% minimum among species % p-distance given the intermixed species pairs in Figure 2.5, but were excluded from this analysis due to too few (n < 2) or too short (< 300 bp) COI sequences.

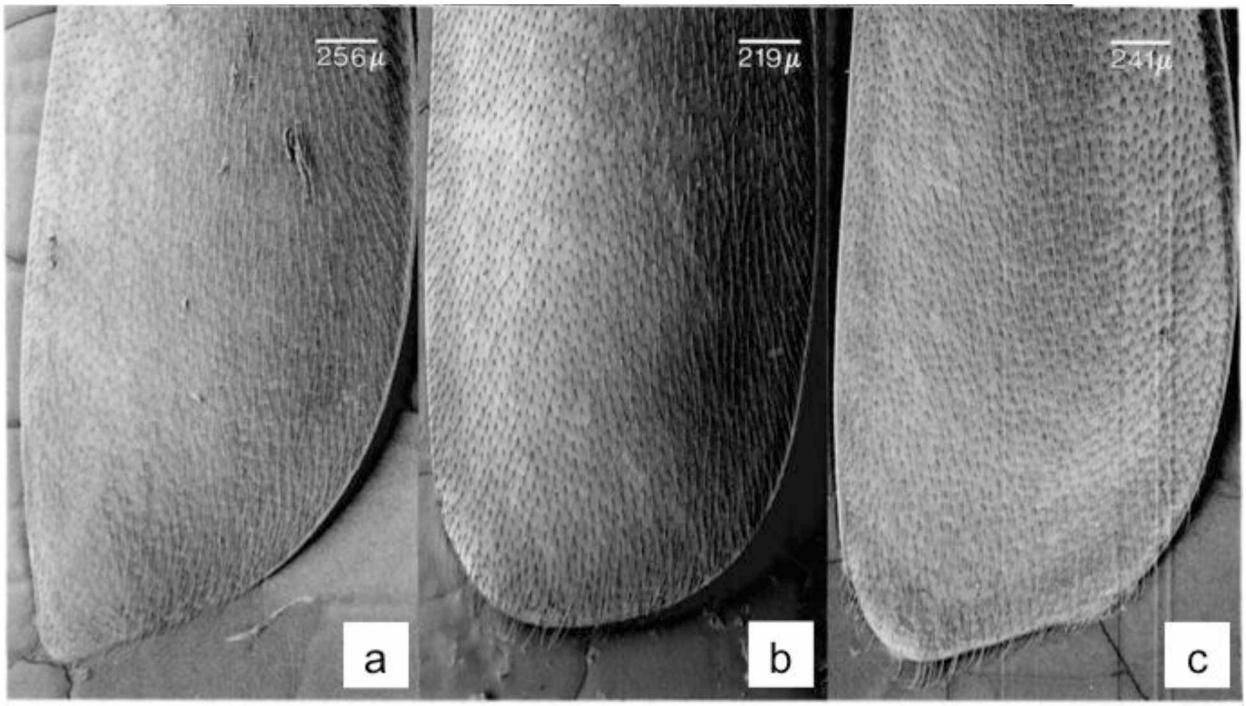

Figure 2.8. Scanning electron microscope images of the elytral apex of A) *Phlaeopterus loganensis*, B) *Phlaeopterus hatchi*, and C) *Phlaeopterus filicornis* female (this species, but not others, is sexually dimorphic in this character). Image modified from Campbell (unpublished).

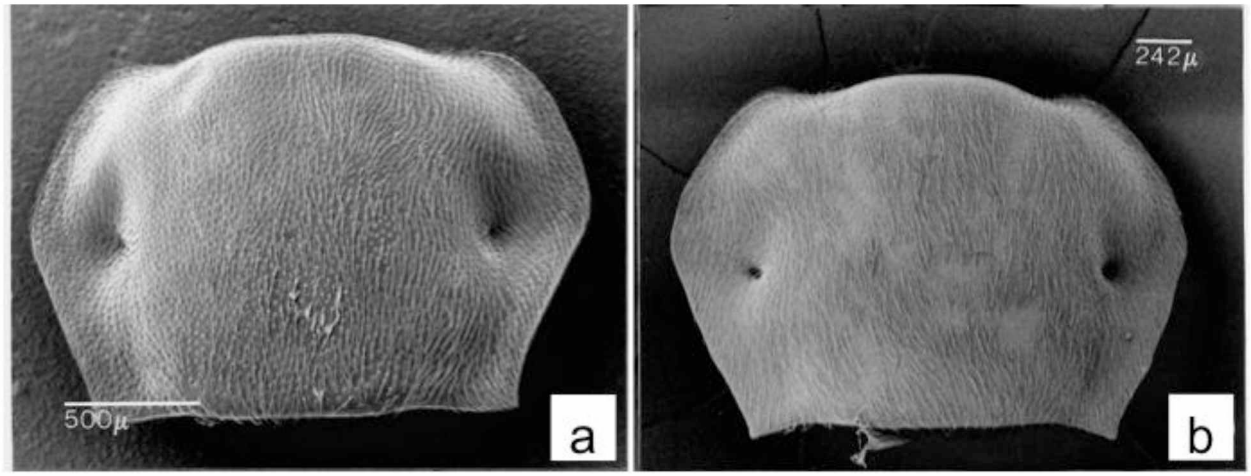

Figure 2.9. Scanning electron microscope images of pronotum of A) *Phlaeopterus cavicollis* and B) *Phlaeopterus occidentallis*.

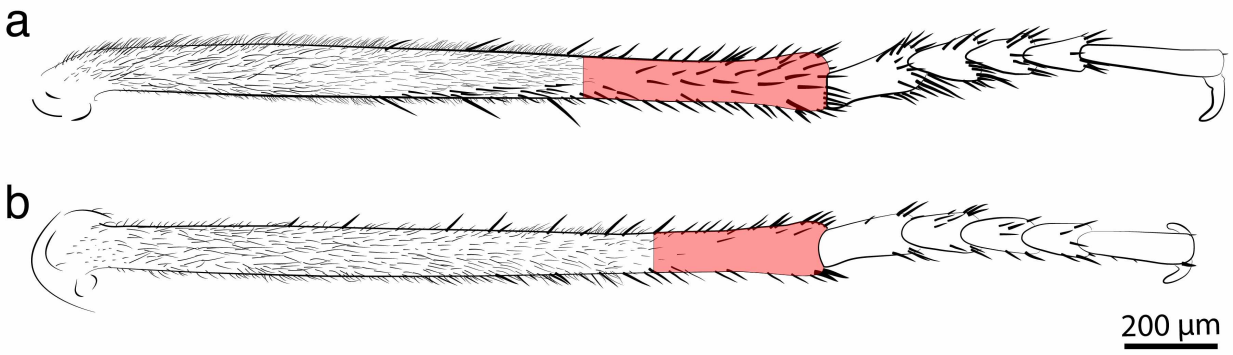

Figure 2.10. Line drawings of mesotibia of A) *Phlaeopterus frosti* UAM10038755211 and B) *Phlaeopterus fusconiger* UAM100399083. Automontage photographs were taken with a Leica MZ16 stereomicroscope and camera, merged in Adobe Photoshop CS6, then traced in Adobe Illustrator. Red highlights were added to illustrate the difference in length of the semi-glabrous region at the apex of the mesotibia.

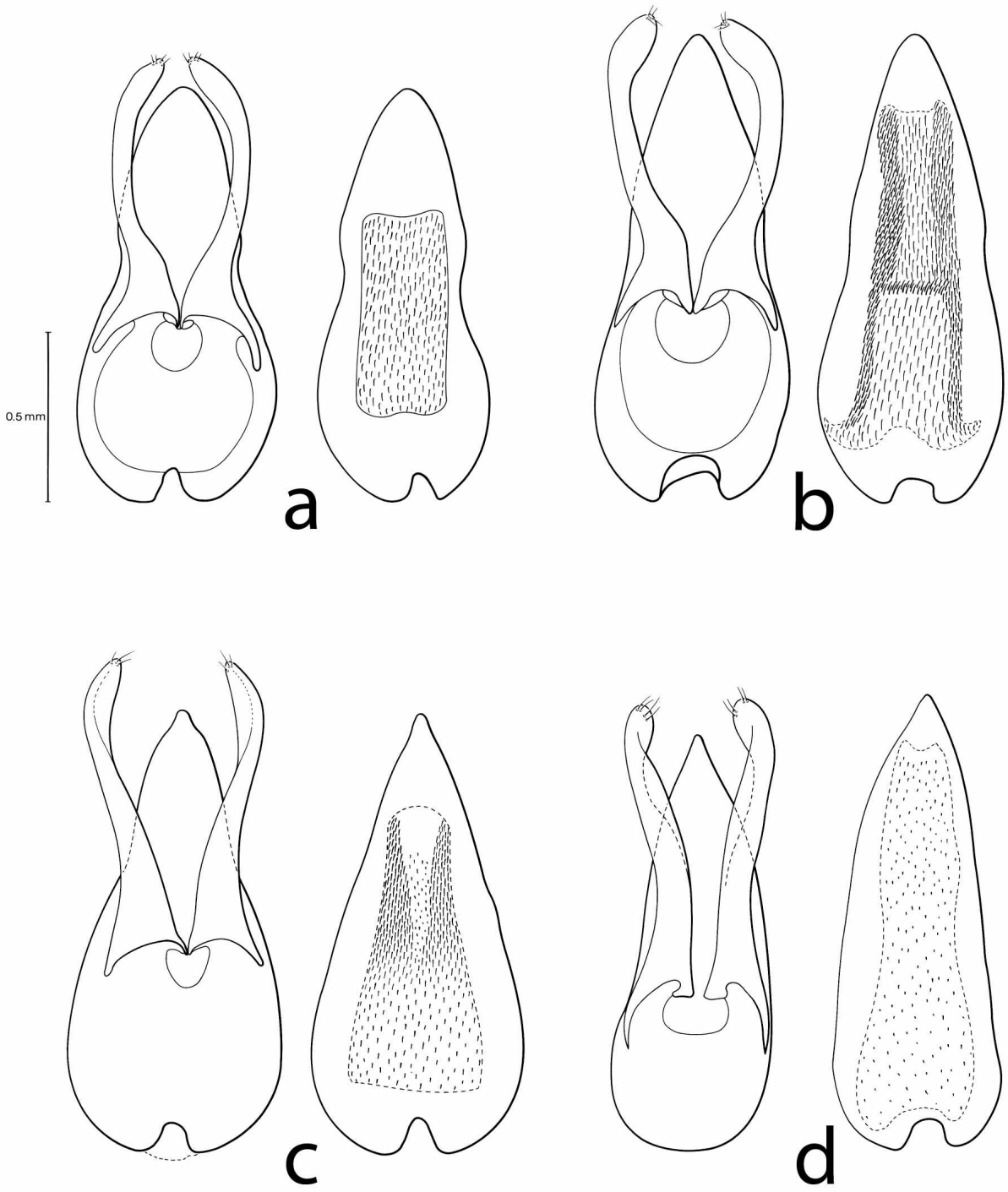

Figure 2.11. Line drawings of male genitalia of A) *Phlaeopterus fusconiger* B) *Phlaeopterus frosti* C) *Phlaeopterus filicornis* and D) *Phlaeopterus hatchi*.

Table 2.1. Summary of approximate elevation range and habitat of *Phlaeopterus* species based on all known collection events as compiled by J.M. Campbell and specimens databased in this study. Localities are the number of locations > 5 km apart (localities < 5 km apart were counted as one locality) a species has been collected based on the > 3,500 specimens georeferenced in this study. Species are sorted by median elevation. Values in parentheses in the elevation range column represent the elevation range most specimens were collected from for species that usually occur in a notably narrower elevation range between the minimum and maximum elevations.

Species	Elevation (m) midpoint	Elevation range (m)	Habitat	Earliest year collected	Latest year collected	# localities
P. frosti	1025	0-2050 (670-2050)	Snowfields, streams and lakes	1905	1987	30
P. lagrandeuri	1100	0-2,200	Snowfields and streams	1905	2013	41
P. houkae	1130	260-2,000	Streams and snowmelt pools	1935	2013	46
P. fusconiger	1220	240-2,200	Snowfields, sometimes streams	1853	2015	29
P. olympicus	1310	650-1,970 (1,500-1,800)	Snowfields, sometimes streams	1927	1984	7
P. czerskyi	1400	900-1,900	Streams	2006	2016	2
P. bakerensis	1460	1,220-1,700	Snowfields	1931	1979	2
P. castaneus	1550	1,000-2,100	Streams, sometimes snowfields	1885	2014	42
P. obsoletus	1550	1,000-2,100	Streams and waterfalls	1905	1996	28
P. occidentalis	1750	300-3,200	Streams and waterfalls	1905	2015	58
P. hatchi	1760	1,360-2,160	Streams, sometimes snowfields	1905	2012	14
P. cavicollis	1935	670-3,200	Snowfields, sometimes streams	1878	2016	75
P. smetanai	1980	360-3,600	Streams and waterfalls	1905	2006	73
P. loganensis	2100	1,650-2,550 (1,900-2,550)	Streams and waterfalls	1893	2010	23
P. elongatus	2150	1,100-3,200	Snowfields, lakes, and streams	1926	2013	7
P. longipennis	2400	1,800-3,000	Streams	1885	2014	19
P. filicornis	2630	1820-3440 (2800-3440)	Snowfields and streams	1886	1990	20
P. kavanaughi	2830	1,830-3,830	Snowfields	1952	2010	12

Table 2.2. Taxonomic hypotheses of the genus *Phlaeopterus*. Hypotheses with "this study" in the author column are *a priori* hypotheses of the authors of this study. Abbreviations: g=genus, sg = informal species group.

Hypothesis	Author	Taxa included
Phlaeopterus g	Motschulsky (1853)	*P. fusconiger*
Phlaeopterus g a synonym of *Lesteva* g	Maklin (1853)	*L. fusconiger* + *Lesteva* Latreille, 1797
Tilea g	Fauvel (1878)	*T. cavicollis*
Vellica g	Casey (1885)	*V. longipennis*
Phlaeopterus g	Casey (1885)	*P. fusconiger, P. longipalpus*
Phlaeopterus g	Casey (1886)	*P. fusconiger, P. longipalpus, P. filicornis*
Phlaeopterus g a synonym of *Tilea* g	Casey (1894)	*T. fusconiger, T. cavicollis, T. longipalpus, T. rufitarsus, T. filicornis, T. brevipennis, T. castaneus*
Tilea g a synonym of *Phlaeopterus g*	Scheerpeltz (1933)	*P. fusconiger, P. cavicollis, P. longipalpus, P. rufitarsus, P. filicornis, P. brevipennis, P. castaneus*
Phlaeopterus g	Hatch (1957)	*Phlaeopterus* g *sensu* Scheerpeltz (1933) + *P. cascadiensis*, *P. frosti*, *P. houkae*, *P. kootenayensis*, *P. lagrandeuri, P. loganensis, P. stacesmithi*
Lesteva g	Shavrin (2001)	*L. czerskyi* + > 100 other spp.
Phlaeopterus g	Shavrin & Mullen (2015)	*Phlaeopterus* g *sensu* Hatch (1957) + *P. czerskyi*
Phlaeopterus g	Mullen *et al.* in prep.	*P. fusconiger, P. cavicollis, P. filicornis, P. castaneus, P. frosti, P. houkae, P. lagrandeuri, P. loganensis, P. longipennis, P. obsoletus, P. kavanaughi, P. bakerensis P. smetanai, P. occidentalis, P. olympicus, P. elongatus P. hatchi, P. czerskyi*
Vellica g a synonym of *Phlaeopterus* g	Mullen *et al.* in prep.	*Phlaeopterus* g *sensu Mullen et al.* in prep. + *P. longipennis*
longipennis sg	this study	*P. longipennis, P. obsoletus*
castaneus sg	this study	*P. castaneus, P. kavanaughi*
cavicollis sg	this study	*P. cavicollis, P. bakerensis, P. smetanai*
fusconiger sg	this study	*P. occidentalis, P. olympicus, P. loganensis, P. fusconiger, P. frosti*
filicornis sg	this study	*P. filicornis, P. hatchi, P. elongatus*

Table 2.3. Morphological dataset containing 46 unordered characters for all 18 *Phlaeopterus* species and 4 *Lesteva* species.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46
L. pubescens	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0
L. longoelytrata	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	?	0	0	0	0	0	0	1	0	0	0	1	0	0	0
L. monticola	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	?	0	0	0	0	0	0	1	0	0	0	1	0	0	0
L. pallipes	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0
P. czerskyi	0	0	2	1	1	2	0	0	?	?	?	1	1	0	?	0	1	1	0	1	2	1	0/1	1	2	2	2	0	0	0	0	2	1	1	1	1	0	0	0	1	2	1	0	1	1	1
P. lagrandeuri	0	0	3	1	1	1	2	0	1	1	1	1	1	0	1	0	2	1	0	1	2	1	0/1	1	2	2	2	1	0	1	0	0	1	1	1	2	1	0	0	1	0	2	1	0	1	2
P. houkae	0	0	2	1	1	1	2	0	1	1	1	1	1	0	1	0	1	2	0	1	3	3	0	1	2	2	2	1	0	1	0	1/2	1	1	1	1	0	0	0	1	0	1	1	0	0	2
P. longipennis	0	0	2	1	1	1	1	0	1	1	1	1	1	0	1	0	2	2	1	1	2	3	0/1	1	2	1	1	0/1	0	1	0	0	1	1	1	1	0	0	0	1	0	1	1	0	0	2
P. obsoletus	0	0	2	1	1	1	1	0	1	1	1	1	1	0	1	0	2	2	1	1	2	3	1	1	2	1	1	0/1	0	1	0	3	1	1	1	1	0	0	0	1	0	1	1	0	0	2
P. filicornis	1	1	2	1	1	2	1	1	1	1	1	1	1	0	1	1	1	1	0	1	2	1	0	0	2	1	1	0	0	1	0/1	3	1	1	1	1	0	1	0	1	0	1	0/1	0	0	1
P. hatchi	1	1	2	1	1	2	1	1	1	1	1	1	1	0	1	1	1	1	0	1	2	1	0	0	1	1	1	0	0	1	0	3	1	1	1	1	0	1	0	1	0	1	0/1	0	0	1
P. elongatus	1	1	2	1	1	2	1	1	1	1	1	1	1	0	1	1	1	1	0	1	2	3	0	0	1	1	1	0	0	1	0	3	1	1	1	1	0	1	0	1	1	1	0/1	0	0	1
P. castaneus	1	2	2	1	1	2	1	1	1	1	1	1	1	0	1	1	1	1	0	1	2	1	0	1	3	1	2	1	0	1	0	3	1	1	1	1	0	0	0	1	0	1	0/1	1	0	1
P. kavanaughi	1	2	2	1	1	2	1	1	1	1	1	1	1	0	1	1	1	1	0	1	2	1	1	1	3	1	2	1	0	1	0	3	1	1	1	1	0	0	0	1	0	1	0/1	1	0	1
P. bakerensis	2	4	2	1	1	2	1	1	1	1	1	1	2	0	1	1	1	1	0	1	2	1	0/1	3	3	1	2	1	1	1	0	3	1	1	1	1	0	3	0	1	0	1	0/1	0	0	1
P. cavicollis	2	4	2	1	1	2	1	1	1	1	1	1	1	0	1	1	1	1	0	1	2	1	1	3	3	1	2	1	0	1	0	3	1	1	1	1	0	3	0	1	0	1	0/1	0	0	1
P. smetanai	2	4	2	1	1	2	1	1	1	1	1	1	1	0	1	1	1	1	0	1	2	1	0	2	3	1	2	1	0	1	0	3	1	1	1	1	0	3	0	1	0	1	0/1	0	0	1
P. occidentalis	1	3	2	1	1	2	1	1	1	1	1	1	1	0	1	1	1	1	0	1	2	1	0/1	1	3	1	2	1	0	1	0	3	1	1	1	1	0	2	0	1	0	1	0/1	0	0	1
P. olympicus	1	3	2	1	1	2	1	1	1	1	1	1	1	0	1	1	1	1	0	1	2	1	0/1	1	3	1	2	1	0	1	0	3	1	1	1	3	0	2	0	1	0	1	0/1	2	0	1
P. loganensis	1	3	2	1	1	2	1	1	1	1	1	1	1	0	1	1	1	1	0	1	2	1	0	1	3	1	2	1	0	3	1	3	1	1	1	3	0	2	0	1	1	1	0/1	0	0	1
P. fusconiger	1	3	2	1	1	2	1	1	1	1	1	1	1	0	1	1	1	1	0	1	2	1	0	1	3	1	2	1	0	1	0	3	1	1	1	1	0	2	0	1	0	1	0/1	0	0	1
P. frosti	1	3	2	1	1	2	1	1	1	1	1	1	1	0	1	1	1	1	0	1	2	1	0	1	3	1	2	1	0	3	0	3	1	1	2	1	0	4	0	1	0	1	0/1	0	0	1

Table 2.4. COI sequences used in this study by locality, University of Alaska Museum Arctos database Global Unique Identifier (UAM GUID), GenBank Accession Number or Barcode of Life Database (BOLD) Process ID, and primers used for COI amplification. Specimen codes include genus and species and correspond to OTU labels in Figures 2.3, 2.4, and 2.5. Locality data has been simplified to save space. Full specimen data is available through arctos.database.museum for those specimens with GUIDs listed.

Specimen Code (used in figures)	Country	State/Providence	Locality	UAM GUID	Genbank or BOLD ID	Primers
Lesteva_longoelytrata_KM440210.1	Germany	North Rhine-Westphalia	Bornheim-Brenig	NA	KM440210.1	LCO1490F/HCO2198R
Lesteva_longoelytrata_KM442270.1	Germany	Rhineland-Palatinate	Kastellaun	NA	KM442270.1	LCO1490F/HCO2198R
Lesteva_monticola_KJ964422.1	Finland	Kolari	Rautuvaara	NA	KJ964422.1	LCO1490F/HCO2198R
Lesteva_monticola_KJ964702.1	Finland	Kolari	Rautuvaara	NA	KJ964702.1	LCO1490F/HCO2198R
Lesteva_pallipes_CNCCJ949.13	Canada	Ontario	Algonquin Provincial Park	NA	ASALC492-13	LCO1490F/HCO2198R
Lesteva_pubescens_KM445870.1	Austria	Tyrol	Dolomiten, Toblach	NA	KM445870.1	LCO1490F/HCO2198R
Phlaeopterus_bakerensis_WA_232776	U.S.A	Washington	Mt. Baker	UAMObs:Ento:232776	forthcomming	Uni-MinibarF1/Uni-MinibarR1
Phlaeopterus_bakerensis_WA_232777	U.S.A	Washington	Mt. Baker	UAMObs:Ento:232777	forthcomming	LepF1/MlepF1-Rev
Phlaeopterus_bakerensis_WA_232782	U.S.A	Washington	Mt. Baker	UAMObs:Ento:232782	forthcomming	LepF1/MlepF1-Rev
Phlaeopterus_bakerensis_WA_232783	U.S.A	Washington	Mt. Baker	UAMObs:Ento:232783	forthcomming	LepF1/MlepF1-Rev
Phlaeopterus_castaneus_AK_132746	U.S.A	Alaska	Flower Mt.	UAM:Ento:132746	UAMIC1108-13	LCO1490F/HCO2198R
Phlaeopterus_castaneus_BBCCN675.10	Canada	British Columbia	Mt. Revelstoke N.P.	UAMObs:Ento:232749	BBCCN675-10	LCO1490F/HCO2198R
Phlaeopterus_castaneus_BC_303785	U.S.A	British Columbia	Geribaldi	UAM:Ento:303785	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_castaneus_CNCCJ964.13	Canada	British Columbia	Manning Prov. Pk.	NA	CNCCJ964-13	LCO1490F/HCO2198R
Phlaeopterus_castaneus_CNCCJ965.13	Canada	British Columbia	Manning Prov. Pk.	NA	CNCCJ965-13	LCO1490F/HCO2198R
Phlaeopterus_castaneus_CNCCJ966.13	U.S.A	Oregon	Hells Cn. N.R.A.	NA	CNCCJ966-13	LCO1490F/HCO2198R
Phlaeopterus_castaneus_CNCCJ967.13	U.S.A	Idaho	Trinity Lks.	NA	CNCCJ967-13	LCO1490F/HCO2198R
Phlaeopterus_castaneus_ID_311977	U.S.A	Idaho	Idaho Co.	UAM:Ento:311977	forthcomming	LepF1/MlepF1-Rev
Phlaeopterus_castaneus_ID_317804	U.S.A	Idaho	Seven Devils Lake	UAM:Ento:317804	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_castaneus_MT_232985	U.S.A	Montana	Glacier N.P.	UAMObs:Ento:232985	forthcomming	LepF1/MlepF1-Rev
Phlaeopterus_castaneus_OR_232989	U.S.A	Oregon	Mt. Hood	UAMObs:Ento:232989	forthcomming	LepF1/MlepF1-Rev
Phlaeopterus_castaneus_OR_232990	U.S.A	Oregon	Mt. Hood	UAMObs:Ento:232990	forthcomming	LepF1/MlepF1-Rev
Phlaeopterus_castaneus_OR_232991	U.S.A	Oregon	Mt. Hood	UAMObs:Ento:232991	forthcomming	LepF1/MlepF1-Rev
Phlaeopterus_castaneus_OR_232992	U.S.A	Oregon	Mt. Hood	UAMObs:Ento:232992	forthcomming	LepF1/MlepF1-Rev
Phlaeopterus_cavicollis_AK_254996	U.S.A	Alaska	Baranof Is.	UAM:Ento:254996	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_cavicollis_AK_256230	U.S.A	Alaska	Mahoney Mt.	UAM:Ento:256230	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_cavicollis_AK_256231	U.S.A	Alaska	Mahoney Mt.	UAM:Ento:256231	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_cavicollis_AK_256233	U.S.A	Alaska	Mahoney Mt.	UAM:Ento:256233	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_cavicollis_AK_256234	U.S.A	Alaska	Mahoney Mt.	UAM:Ento:256234	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_cavicollis_AK_256238	U.S.A	Alaska	Mahoney Mt.	UAM:Ento:256238	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_cavicollis_AK_256241	U.S.A	Alaska	Mahoney Mt.	UAM:Ento:256241	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_cavicollis_AK_256251	U.S.A	Alaska	Mahoney Mt.	UAM:Ento:256251	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_cavicollis_AK_275765	U.S.A	Alaska	Mahoney Mt.	UAM:Ento:275765	UAMIC2374-14	LCO1490F/HCO2198R
Phlaeopterus_cavicollis_AK_275766	U.S.A	Alaska	Hawthorne Peak	UAM:Ento:275766	UAMIC2294-14	LCO1490F/HCO2198R
Phlaeopterus_cavicollis_CA_231988	U.S.A	California	Riverside Co.	UAMObs:Ento:231988	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_cavicollis_CA_232004	U.S.A	California	Nevada Co.	UAMObs:Ento:232004	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_cavicollis_CA_232735	U.S.A	California	Trinity Alps	UAMObs:Ento:232735	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_cavicollis_CA_232736	U.S.A	California	Lilly Lake	UAMObs:Ento:232736	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_cavicollis_CA_232737	U.S.A	California	Trinity Alps	UAMObs:Ento:232737	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_cavicollis_CA_232738	U.S.A	California	Trinity Alps	UAMObs:Ento:232738	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_cavicollis_CA_232739	U.S.A	California	Trinity Alps	UAMObs:Ento:232739	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_cavicollis_CNCCJ968.13	Canada	British Columbia	Garibaldi Prov. Pk.	NA	CNCCJ968-13	LCO1490F/HCO2198R
Phlaeopterus_cavicollis_CNCCJ969.13	Canada	British Columbia	Manning Prov. Pk.	NA	CNCCJ969-13	LCO1490F/HCO2198R
Phlaeopterus_cavicollis_CNCCJ970.13	Canada	Alberta	Waterton Lks. N.P.	NA	CNCCJ970-13	LCO1490F/HCO2198R
Phlaeopterus_cavicollis_OR_311979	U.S.A	Oregon	Baker Co.	UAM:Ento:311979	forthcomming	LepF1/MlepF1-Rev
Phlaeopterus_cavicollis_WA_232734	U.S.A	Washington	Olympic N.P.	UAMObs:Ento:232734	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_cavicollis_WA_232741	U.S.A	Washington	Olympic N.P.	UAMObs:Ento:232741	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_czerskyi_RUS_232770	Russia	Russia	Eastern Siberia	UAMObs:Ento:232770	forthcomming	LepF1/MlepF1-Rev
Phlaeopterus_elongatus_AK_303798	U.S.A	Alaska	Alaska Range	UAM:Ento:303798	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_elongatus_AK_303799	U.S.A	Alaska	Alaska Range	UAM:Ento:303799	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_elongatus_AK_303801	U.S.A	Alaska	Alaska Range	UAM:Ento:303801	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_elongatus_AK_303802	U.S.A	Alaska	Alaska Range	UAM:Ento:303802	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_elongatus_AK_303803	U.S.A	Alaska	Hatcher Pass	UAM:Ento:303803	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_elongatus_AK_303804	U.S.A	Alaska	Hatcher Pass	UAM:Ento:303804	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_elongatus_AK_303805	U.S.A	Alaska	Hatcher Pass	UAM:Ento:303805	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_elongatus_AK_303806	U.S.A	Alaska	Hatcher Pass	UAM:Ento:303806	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_elongatus_AK_303810	U.S.A	Alaska	Hatcher Pass	UAM:Ento:303810	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_elongatus_AK_303811	U.S.A	Alaska	Hatcher Pass	UAM:Ento:303811	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_filicornis_CA_233113	U.S.A	California	Mono Co.	UAMObs:Ento:233113	forthcomming	LepF1/MlepF1-Rev
Phlaeopterus_filicornis_MT_232983	U.S.A	Montana	Glacier N.P.	UAMObs:Ento:232983	forthcomming	LepF1/MlepF1-Rev
Phlaeopterus_filicornis_MT_232988	U.S.A	Montana	Glacier N.P.	UAMObs:Ento:232988	forthcomming	LepF1/MlepF1-Rev
Phlaeopterus_frosti_CNCCJ981.13	U.S.A	Washington	Mt. Baker	NA	CNCCJ981-13	LCO1490F/HCO2198R
Phlaeopterus_frosti_CNCCJ982.13	Canada	British Columbia	Manning Prov. Pk.	NA	CNCCJ982-13	LCO1490F/HCO2198R

Table 2.4 continued.

Specimen Code (used in figures)	Country	State/Providence	Locality	UAM GUID	Genbank or BOLD ID	Primers
Phlaeopterus_fuscongier_CNCCJ976.13	Canada	British Columbia	Queen Charlotte Is.	NA	CNCCJ976-13	LCO1490F/HCO2198R
Phlaeopterus_fusconiger_AK_147759	U.S.A	Alaska	S. Chilkat Pen.	UAM:Ento:147759	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_fusconiger_AK_147764	U.S.A	Alaska	S. Chilkat Pen.	UAM:Ento:147764	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_fusconiger_AK_147808	U.S.A	Alaska	S. Chilkat Pen.	UAM:Ento:147808	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_fusconiger_AK_147810	U.S.A	Alaska	S. Chilkat Pen.	UAM:Ento:147810	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_fusconiger_AK_149862	U.S.A	Alaska	Heintzleman Ridge	UAM:Ento:149862	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_fusconiger_AK_149863	U.S.A	Alaska	Heintzleman Ridge	UAM:Ento:149863	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_fusconiger_AK_149864	U.S.A	Alaska	Heintzleman Ridge	UAM:Ento:149864	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_fusconiger_AK_149865	U.S.A	Alaska	Heintzleman Ridge	UAM:Ento:149865	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_fusconiger_AK_149916	U.S.A	Alaska	Heintzleman Ridge	UAM:Ento:149916	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_fusconiger_AK_150994	U.S.A	Alaska	Heintzleman Ridge	UAM:Ento:150994	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_fusconiger_AK_151000	U.S.A	Alaska	Heintzleman Ridge	UAM:Ento:151000	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_fusconiger_AK_151001	U.S.A	Alaska	Heintzleman Ridge	UAM:Ento:151001	UAMIC1120-13	LCO1490F/HCO2198R
Phlaeopterus_fusconiger_AK_151002	U.S.A	Alaska	Heintzleman Ridge	UAM:Ento:151002	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_fusconiger_AK_151003	U.S.A	Alaska	Heintzleman Ridge	UAM:Ento:151003	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_fusconiger_AK_151004	U.S.A	Alaska	Heintzleman Ridge	UAM:Ento:151004	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_fusconiger_AK_151005	U.S.A	Alaska	Heintzleman Ridge	UAM:Ento:151005	UAMIC1121-13	LCO1490F/HCO2198R
Phlaeopterus_fusconiger_AK_151006	U.S.A	Alaska	Heintzleman Ridge	UAM:Ento:151006	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_fusconiger_AK_151007	U.S.A	Alaska	Heintzleman Ridge	UAM:Ento:151007	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_fusconiger_AK_232740	U.S.A	Alaska	Olympic N.P.	UAMObs:Ento:232740	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_fusconiger_AK_258286	U.S.A	Alaska	Chichagof Is.	UAM:Ento:258286	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_fusconiger_AK_303814	U.S.A	Alaska	Haines	UAM:Ento:303814	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_fusconiger_AK_303815	U.S.A	Alaska	Haines	UAM:Ento:303815	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_fusconiger_AK_303817	U.S.A	Alaska	Haines	UAM:Ento:303817	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_fusconiger_AK_303818	U.S.A	Alaska	Haines	UAM:Ento:303818	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_fusconiger_AK_303819	U.S.A	Alaska	Haines	UAM:Ento:303819	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_fusconiger_AK_303822	U.S.A	Alaska	Haines	UAM:Ento:303822	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_fusconiger_AK_303823	U.S.A	Alaska	Haines	UAM:Ento:303823	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_fusconiger_AK_303824	U.S.A	Alaska	Haines	UAM:Ento:303824	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_fusconiger_AK_303825	U.S.A	Alaska	Haines	UAM:Ento:303825	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_fusconiger_AK_303827	U.S.A	Alaska	Haines	UAM:Ento:303827	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_fusconiger_AK_303828	U.S.A	Alaska	Haines	UAM:Ento:303828	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_fusconiger_AK_303829	U.S.A	Alaska	Paradise Valley	UAM:Ento:303829	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_fusconiger_AK_317327	U.S.A	Alaska	Adak Island	UAM:Ento:317327	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_fusconiger_AK_317328	U.S.A	Alaska	Adak Island	UAM:Ento:317328	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_fusconiger_AK_317329	U.S.A	Alaska	Adak Island	UAM:Ento:317329	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_fusconiger_AK_317330	U.S.A	Alaska	Adak Island	UAM:Ento:317330	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_fusconiger_CNCCJ977.13	Canada	British Columbia	Queen Charlotte Is.	NA	CNCCJ977-13	LCO1490F/HCO2198R
Phlaeopterus_fusconiger_CNCCJ978.13	U.S.A	Alaska	Alaska Range	NA	CNCCJ978-13	LCO1490F/HCO2198R
Phlaeopterus_fusconiger_CNCCJ979.13	U.S.A	Alaska	Kenai Mts.	NA	CNCCJ979-13	LCO1490F/HCO2198R
Phlaeopterus_hatchi_AK_232742	U.S.A	Alaska	Juneau	UAM:Ento:232742	forthcomming	LepF1/MlepF1-Rev
Phlaeopterus_houkae_AK_152322	U.S.A	Alaska	Juneau	UAM:Ento:152322	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_houkae_AK_258968	U.S.A	Alaska	Chicagof Island	UAM:Ento:258968	UAMIC2327-14	LCO1490F/HCO2198R
Phlaeopterus_houkae_AK_275535	U.S.A	Alaska	Juneau	UAM:Ento:275535	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_houkae_AK_275545	U.S.A	Alaska	Juneau	UAM:Ento:275545	UAMIC2293-14	LCO1490F/HCO2198R
Phlaeopterus_houkae_CNCCJ959.13	U.S.A	Washington	Mt. Rainier N.P.	NA	CNCCJ959-13	LCO1490F/HCO2198R
Phlaeopterus_houkae_CNCCJ960.13	Canada	British Columbia	Terrace	NA	CNCCJ960-13	LCO1490F/HCO2198R
Phlaeopterus_houkae_CNCCJ962.13	U.S.A	Alaska	Alaska Range	NA	CNCCJ962-13	LCO1490F/HCO2198R
Phlaeopterus_kavanaughi_CA_232733	U.S.A	California	Trinity Alps	UAMObs:Ento:232733	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_kavanaughi_CA_232743	U.S.A	California	Yosemite N.P.	UAMObs:Ento:232743	forthcomming	LepF1/MlepF1-Rev
Phlaeopterus_kavanaughi_CA_232745	U.S.A	California	Yosemite N.P.	UAMObs:Ento:232745	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_lagrandeuri_BC_303784	Canada	British Columbia	Geribaldi	UAM:Ento:303784	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_lagrandeuri_CNCCJ955.13	U.S.A	Oregon	Mary's Peak	NA	CNCCJ955.13	LCO1490F/HCO2198R
Phlaeopterus_lagrandeuri_CNCCJ956.13	Canada	British Columbia	Queen Charlotte Is.	NA	CNCCJ956.13	LCO1490F/HCO2198R
Phlaeopterus_lagrandeuri_UAMIC1845.:	U.S.A	Alaska	Prince of Wales Is.	UAM:Ento:221393	UAMIC1845.14	LCO1490F/HCO2198R
Phlaeopterus_lagrandeuri_UAMIC632.1:	U.S.A	Alaska	Prince of Wales Is.	UAM:Ento:203074	UAMIC632.13	LCO1490F/HCO2198R
Phlaeopterus_lagrandeuri_UAMIC633.1:	U.S.A	Alaska	Prince of Wales Is.	UAM:Ento:203075	UAMIC633.13	LCO1490F/HCO2198R
Phlaeopterus_lagrandeuri_WA_232762	U.S.A	Washington	Spokane	UAMObs:Ento:232762	forthcomming	LepF1/MlepF1-Rev
Phlaeopterus_lagrandeuri_WA_232765	U.S.A	Washington	Spokane	UAMObs:Ento:232765	forthcomming	LepF1/MlepF1-Rev
Phlaeopterus_loganensis_BBCCN358.10	Canada	Alberta	Jasper N.P.	UAMObs:Ento:232748	BBCCN358-10	LCO1490F/HCO2198R
Phlaeopterus_loganensis_CNCCJ972.13	Canada	British Columbia	Mt. Revelstoke N.P.	NA	CNCCJ972-13	LCO1490F/HCO2198R
Phlaeopterus_loganensis_CNCCJ973.13	Canada	Alberta	Waterton Lks. N.P.	NA	CNCCJ973-13	LCO1490F/HCO2198R
Phlaeopterus_loganensis_CNCCJ974.13	Canada	Alberta	Waterton Lks. N.P.	NA	CNCCJ974-13	LCO1490F/HCO2198R
Phlaeopterus_loganensis_CNCCJ975.13	U.S.A	Montana	Silvertip Mt.	NA	CNCCJ975-13	LCO1490F/HCO2198R
Phlaeopterus_loganensis_MT_232982	U.S.A	Montana	Glacier N.P.	UAMObs:Ento:232982	forthcomming	LepF1/MlepF1-Rev
Phlaeopterus_longipennis_fem_68903f	U.S.A	Oregon	Mt. Hood N.F.	NA	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_longipennis_mal_68903f	U.S.A	Oregon	Mt. Hood N.F.	NA	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_longipennis_OR_234973	U.S.A	Oregon	Mt. Hood	UAMObs:Ento:234973	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_longipennis_OR_234974	U.S.A	Oregon	Mt. Hood	UAMObs:Ento:234974	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_occidentalis_CA_231996	U.S.A	California	Kern Co.	UAMObs:Ento:231996	forthcomming	LCO1490F/HCO2198R
Phlaeopterus_occidentalis_NV_231968	U.S.A	Nevada	San Bernardino Co.	UAMObs:Ento:231968	forthcomming	LepF1/MlepF1-Rev
Phlaeopterus_olympicus_WA_232778	U.S.A	Washington	Olympic N.P.	UAMObs:Ento:232778	forthcomming	LepF1/MlepF1-Rev
Phlaeopterus_olympicus_WA_232779	U.S.A	Washington	Olympic N.P.	UAMObs:Ento:232779	forthcomming	LepF1/MlepF1-Rev
Phlaeopterus_olympicus_WA_232780	U.S.A	Washington	Olympic N.P.	UAMObs:Ento:232780	forthcomming	LepF1/MlepF1-Rev
Phlaeopterus_olympicus_WA_232781	U.S.A	Washington	Olympic N.P.	UAMObs:Ento:232781	forthcomming	Uni-MinibarF1/Uni-MinibarR1
Phlaeopterus_smetanai_CA_232907	U.S.A	California	Mount Lassen	UAMObs:Ento:232907	forthcomming	Uni-MinibarF1/Uni-MinibarR1
Phlaeopterus_smetanai_UT_232772	U.S.A	Utah	Wasatach Co.	UAMObs:Ento:232772	forthcomming	Uni-MinibarF1/Uni-MinibarR1
Phlaeopterus_smetanai_UT_232775	U.S.A	Utah	Wasatach Co.	UAMObs:Ento:232775	forthcomming	Uni-MinibarF1/Uni-MinibarR1

Table 2.5. Sequence for primers, target sequence length in base pairs, and original authors of primers used in this study.

Primer	Target Sequence (5'-3')	Paired With	Target Length (bp)	Source
LCO-1490	GGTCAACAAATCATAAAGATATTGG	HCO-2198	658	Folmer *et al.* (1994)
HCO-2198	TAAACTTCAGGGTGACCAAAAAATCA	LCO-1490		Folmer *et al.* (1994)
LepF1	ATTCAACCAATCATAAAGATATTGG	MLepF1-Rev	211	Hebert *et al.* (2004)
MLepF1-Rev	CGTGGAAAWGCTATATCWGGTG	LepF1		Brandon-Mong *et al.* (2015)
Uni-MinibarF1	TCCACTAATCACAARGATATTGGTAC	Uni-MinibarR1	133	Meusnier *et al.* (2008)
Uni-MinibarR1	GAAAATCATAATGAAGGCATGAGC	Uni-MinibarF1		Meusnier *et al.* (2008)

Table 2.6. Testing taxonomic hypotheses of the genus *Phlaeopterus* using Bayesian morphology-only (Fig. 2.6), COI-only (Fig. 2.4), and COI+morphology (Fig. 2.3) phylogenies. Hypotheses with "this study" in the author column are the *a priori* hypotheses of the authors of this study, and were originally conceived by J. M. Campbell. Groups are marked with an asterisk (*) if recovered as polyphyletic and a plus sign (+) if recovered as paraphyletic. Taxa included in each group are listed in Table 2.2 and our *a priori* hypotheses are also indicated on the morphology-only phylogeny (Fig. 2.6). Clades that did not occur in any of the sampled trees in an MCMCMC run were assumed to have a posterior probability of < 1/number of trees sampled (in this case < 0.0001). Abbreviations: g = genus, sg = informal species group, "-"= untested because of monotypy (too few data).

Hypothesis	Author	Posterior probability morphology	Posterior probability COI	Posterior probability morphology + COI
Phlaeopterus g	Motschulsky (1853)	-	-	-
Phlaeopterus g a synonym of *Lesteva* g	Maklin (1853)	-	-	-
Tilea g	Fauvel (1878)	-	-	-
Vellica g	Casey (1885)	-	-	-
Phlaeopterus g	Casey (1885)	1.00	0.96	0.60
Phlaeopterus g	Casey (1886)	1.00	0.63	0.99
Phlaeopterus g a synonym of *Tilea g*	Casey (1894)	1.00	0.63	0.99
Tilea g a synonym of *Phlaeopterus g*	Scheerpeltz (1933)	1.00	0.63	0.99
Phlaeopterus g	Hatch (1957)	1.00	0.63	0.60
Lesteva g	Shavrin (2001)	<0.0001*	<0.0001*	<0.0001*
Phlaeopterus g	Shavrin & Mullen (2015)	0.92	0.96	1.00
Phlaeopterus g	Mullen *et al.* in prep.	1.00	0.96	1.00
Vellica g a synonym of *Phlaeopterus* g	Mullen *et al.* in prep.	1.00	0.96	1.00
longipennis sg	this study	0.93	-	1.00
castaneus sg	this study	0.90	<0.0001*	0.58
cavicollis sg	this study	0.98	<0.0001*	0.53
fusconiger sg	this study	0.27+	<0.0001*	<0.0001*
filicornis sg	this study	0.99	<0.0001+	0.99

Table 2.7. Base composition, total number of sites, and number of informative sites for the full COI dataset, the in-group dataset (*Phlaeopterus* only), full COI dataset by codon position and "short" COI sequences (133–218 bp in length sequenced using LepF1/MLepF1-Rev and Uni-MinibarF1/Uni-MinibarR1 primer sets. All statistics calculated with PAUP* 4.0.

	%A	%C	%G	%T	Sites (n)	Informative Sites (n)
COI full	29.72	17.17	16.47	36.65	658	195
COI ingroup	30.48	16.2	16.73	36.59	658	170
COI 1st	29.22	17.49	29.5	23.8	219	31
COI 2nd	13.63	25.46	17.84	43.08	219	1
COI 3rd	46.3	8.56	2.08	43.06	220	163
COI "short"	28.78	16.54	18.25	36.43	241	44

Literature Cited

Brandon-Mong, G.J., Gan, H.M., Sing, K.W., Lee, P.S., Lim, P.E. and Wilson, J.J., 2015. DNA metabarcoding of insects and allies: an evaluation of primers and pipelines. Bulletin of entomological research, 105(6), pp.717-727.

Campbell, J.M., 1978. A revision of the North American Omaliinae (Coleoptera: Staphylinidae) 1. The genera *Haida* Keen, *Pseudohaida* Hatch, and *Eudectoides* new genus. *Memoirs of the Entomological Society of Canada*, 110(106), 1–20.

Campbell, J.M., 1982. A revision of the North American Omaliinae (Coleoptera: Staphylinidae): 3. The genus *Acidota* Stephens. *The Canadian Entomologist*, 114(11), 1003–1029.

Campbell, J.M., 1983. A revision of the North American Omaliinae (Coleoptera: Staphylinidae): 4. The genus *Olophrum* Erichson. *The Canadian Entomologist,* 115(6), 577–622.

Campbell, J.M., 1984. A revision of the North American Omaliinae (Coleoptera: Staphylinidae): 5. The genera *Arpedium* Erichson and *Eucnecosum* Reitter. *The Canadian Entomologist,* 11(6), 487–527.

Casey, T.L., 1885. New genera and species of Californian Coleoptera. *Bulletin of the California Academy of Sciences*, 7, 281–606.

Casey, T.L., 1886. Descriptive notices of North American Coleoptera I. *Bulletin of the California Academy of Sciences,* 2(6), 157–264.

Casey, T.L., 1893. Coleopterological Notices V. *Annals of the New York Academy of Sciences*, 7(1), 281–624.

Casey, T.L., 1894. Coleopterological Notices VI. *Annals of the New York Academy of Sciences*, 8(1), 435–838.

Cognato, A.I., 2006. Standard percent DNA sequence difference for insects does not predict species boundaries. *Journal of Economic Entomology*, 99(4), 1037–1045.

Darriba D., Taboada G.L., Doallo R., Posada D.. 2012. jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods,* 9(8), 772.

Douady, C.J., Delsuc, F., Boucher, Y., Doolittle, W.F., Douzery, E.J., 2003. Comparison of Bayesian and maximum likelihood bootstrap measures of phylogenetic reliability. *Molecular Biology and Evolution*, 20(2), 248–254.

Dowton, M., Austin, A.D., 1997. Evidence for AT-transversion bias in wasp (Hymenoptera: Symphyta) mitochondrial genes and its implications for the origin of parasitism. *Journal of Molecular Evolution*, 44(4), 398–405.

Erixon, P., Svennblad, B., Britton, T., Oxelman, B., 2003. Reliability of Bayesian posterior probabilities and bootstrap frequencies in phylogenetics. *Systematic Biology*, 52(5), 665–673.

Fauvel, A., 1878. Les Staphylinides de l'Amerique du Nord. *Notices Entomologiques* 7, 1–100.

Folmer, O., Black, M., Hoeh, W., Lutz, R., Vrijenhoek, R., 1994. DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Molecular Marine Biology and Biotechnology*, *3*(5), 294–299.

Funk, D.J. and Omland, K.E., 2003. Species-level paraphyly and polyphyly: frequency, causes, and consequences, with insights from animal mitochondrial DNA. *Annual Review of Ecology, Evolution, and Systematics*, 34(1), 397-423.

Goeze, J.A.E., 1777. Entomologische Beyträge, Leipzig.

Griekspoor, A., and Groothuis, T., 2005. 4Peaks, version 1.7. Nucleobytes.com.

Hatch, M.H., 1957. The beetles of the Pacific Northwest: Part II: Staphyliniformia. University of Washington Press: Seattle, WA, USA.

Hebert, P.D.N., Penton, E.H., Burns, J.M., Janzen, D.H., Hallwachs, W., 2004. Ten species in one: DNA barcoding reveals cryptic species in the neotropical skipper butterfly *Astraptes fulgerator*. *Proceedings of the National Academy of Sciences of the United States of America*, 101(41), 14812–14817.

Hendrich, L., Morinière, J., Haszprunar, G., Hebert, P.D., Hausmann, A., Köhler, F., Balke, M., 2015. A comprehensive DNA barcode database for Central European beetles with a focus on Germany: adding more than 3500 identified species to BOLD. *Molecular Ecology Resources*, 15(4), 795-818.

Hennig, W., 1966. Phylogenetic systematics. University of Illinois Press, Urbana. 263 pp.

Herman, L.H., 2001. Catalog of the Staphylinidae (Insecta: Coleoptera). 1758 to the end of the second millenium. I. Introduction, history, biogeographical sketches, and Omaliine group. *Bulletin of the American Museum of Natural History*, 265, 1–650.

Hillis, D.M., and Wiens, J.J., 2000. Molecules versus morphology in systematics: conflicts, artifacts, and misconceptions. In 'Phylogenetic Analysis of Morphological Data'. (Ed. J. Wiens.) Smithsonian Institution Press: Washington, DC. pp. 1–19.

Huelsenbeck, J.P. and Rannala, B., 2004. Frequentist properties of Bayesian posterior probabilities of phylogenetic trees under simple and complex substitution models. *Systematic biology*, 53(6), 904-913.

Kass, R.E. and Raftery, A.E., 1995. Bayes factors. *Journal of the American Statistical Association*, 90(430), 773–795.

Kubatko, L.S., Degnan, J.H., 2007. Inconsistency of phylogenetic estimates from concatenated data under coalescence. *Systematic Biology*, 56(1), 17–24.

Lanfear R., Calcott, B., Ho, S.Y.W., Guindon S., 2012. PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution*, 29(6), 1695–1701.

Latreille, P.A., 1797. *Precis des caracteres generiques des insectes, disposes dans un ordre naturel xiv*, Bourdeaux, Brive, France.

Lewis, P.O., 2001. A likelihood approach to estimating phylogeny from discrete morphological character data. *Systematic Biology*, 50(6), 913–925.

Macleay, W.S., Horsfield, T., 1825. Annulosa javanica, or, an attempt to illustrate the natural affinities and analogies of the insects collected in Java by Thomas Horsfield.

Maddison, W.P., 1997. Gene trees in species trees. *Systematic Biology*, 46(3), 523–536.

Maddison, D.R. and Maddison, W.P., 2005. MacClade 4: Analysis of phylogeny and character evolution. Version 4.08 a.

Maddison, W.P., Maddison, D.R., 2016. Mesquite: a modular system for evolutionary analysis. Version 3.10 http://mesquiteproject.org

Mäklin, F.G., 1853. [New species and notes]. In: Mannerheim, C.v., Dritter Nachtrag zur Kaefer-Fauna der Nord- Amerikanischen Laender des Russischen Reiches. *Bulletin de la Société Impériale des Naturalistes de Moscou*, 26(3 & 4), 95–273.

Meusnier, I., Singer, G.A., Landry, J.F., Hickey, D.A., Hebert, P.D.N., Hajibabaei, M. 2008. A universal DNA mini-barcode for biodiversity analysis. *BMC Genomics*, 9(1), 214.

Miller, M.A., Pfeiffer, W. and Schwartz, T., 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: Gateway Computing Environments Workshop (GCE), 1–8.

Miller, R.E., Buckley, T.R., Manos, P.S., 2002. An examination of the monophyly of morning glory taxa using Bayesian phylogenetic inference. *Systematic Biology*, 51(5), 740–7533.

Moore, I., Legner, E.F. 1979 An illustrated guide to the genera of the Staphylinidae of America North of Mexico exclusive of the Aleocharinae (Coleoptera). Division of Agricultural Sciences, University of California Priced Publication, 4093, 332 pg.

Motschulsky, V.I., 1853. *Etudes Entomologiques*. La Société de Litérature Finnoise: Helsinki, Finland.

Moulton, J.K., Wiegmann, B.M., 2004. Evolution and phylogenetic utility of CAD (rudimentary) among Mesozoic-aged Eremoneuran Diptera (Insecta). *Molecular phylogenetics and evolution*, 31(1), 363–78.

Newton, A.F., Thayer, M.K., Ashe, J.S., Chandler, D.S., 2000. 22. Staphylinidae Latreille, 1802. *In: Arnett, R.H. & Thomas, M.C. (Ed.), American Beetles, Vol. 1. Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia*, 272–418.

Rambaut, A., Suchard, M.A., Xie, D., Drummond A.J., 2014, Tracer v1.6, Available at: http://beast.bio.ed.ac.uk/Tracer

Rodríguez, F., Oliver, J.F., Marín, A., Medina, J.R., 1990. The general stochastic model of nucleotide substitution. *Journal of Theoretical Biology,* 142(4), 485–501.

Ricker, W.E., 1952. Systematic studies of Plecoptera. Indiana University Publishing Science Services, 18, 1–200.

Ronquist, F., Teslenko, M., Van Der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. and Huelsenbeck, J.P., 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61(3), 539–542.

Scheerpeltz, O., 1933. Staphylinidae VII. In: Schenkling, S. (Ed.), *Coleopterorum Catalogus*, 129, 989–1500. [Berlin: Junk]

Shavrin, A.V., 2001. New and little-known species of Omaliinae from the Baikal-Transbaikal area (Coleoptera: Staphylinidae). *Zoosystematica Rossica*, 9(1), 189–193.

Shavrin, A.V., 2010. Three new species of the genus Lesteva Latreille, 1797 (Coleoptera: Staphylinidae: Omaliinae: Anthophagini) from Uzbekistan, Tadzhikistan and Afghanistan. *Baltic Journal of Coleopterology*, 10(2), 147–152.

Shavrin, A.V., 2014. Review of the genus *Lesteva* Latreille, 1797 (Coleoptera: Staphylinidae: Omaliinae: Anthophagini) of Iran and adjacent territories. *Zootaxa*, 3884(2), 122–140.

Shavrin, A.V., 2015. New data on Himalayan *Lesteva* Latreille, 1797 (Coleoptera: Staphylinidae: Omaliinae) with description of a new species from Nepal. *Zootaxa*, 3973(3), 528.

Shavrin, A.V., Mullen, L.J., 2015. *Phlaeopterus* Motschulsky, 1853 (Coleoptera: Staphylinidae: Omaliinae: Anthophagini)-a new genus for the Palaearctic: new combination. *Zootaxa*, 4028(1), 121–128.

Shavrin, A.V., Shilenkov, V.G. and Anistschenko, A.V., 2007. Two new species and additional records of Lesteva Latreille, 1797 from the mountains of South Siberia (Coleoptera: Staphylinidae: Omaliinae: Anthophagini). *Zootaxa*, 1427(1), 37–47.

Swofford, D.L., 2003. PAUP*: phylogenetic analysis using parsimony, version 4.0 b10.

Thomson, C.G. 1859. Skandinaviens Coleoptera, synoptiskt bearbetade, vol. 1. Berlingska Boktryckeriet, Lund, 290 pp.

Trewick, S.A., 2008. DNA Barcoding is not enough: mismatch of taxonomy and genealogy in New Zealand grasshoppers (Orthoptera: Acrididae).*Cladistics*, *24*(2), 240-254.

Whitworth, T. L., Dawson, R.D., Magalon, H., Baudry, E., 2007. DNA barcoding cannot reliably identify species of the blowfly genus *Protocalliphora* (Diptera: Calliphoridae). *Proceedings of the Royal Society of London B: Biological Sciences,* 274(1619), 1731–1739.

Wiens, J. J., 2004. The role of morphological data in phylogeny reconstruction. *Systematic Biology*, 53(4), 653–61. http://doi.org/10.1080/10635150490472959

Wiens, J.J., Penkrot, T.A., 2002. Delimiting species using DNA and morphological variation and discordant species limits in spiny lizards (*Sceloporus*). *Systematic Biology*, 51(1), 69–91.

Wright, A.M. and Hillis, D.M., 2014. Bayesian analysis using a simple likelihood model outperforms parsimony for estimation of phylogeny from discrete morphological data. *PLoS One*, 9(10), e109210.

Xia, X., Xie, Z., Salemi, M., Chen, L. and Wang, Y., 2003. An index of substitution saturation and its application. *Molecular phylogenetics and evolution*, 26(1), pp.1-7.

Xia, X. and Lemey, P., 2009. Assessing substitution saturation with DAMBE. The phylogenetic handbook: a practical approach to DNA and protein phylogeny, 2, pp.615-630.

Yang, Z., 1994. Maximum likelihood phylogenetic estimation from DNA sequences with variable rates over sites: approximate methods. *Journal of Molecular Evolution* 39(3), 306–314.

Zwickl, D.J., 2006. Genetic algorithm approaches for the phylogenetic analysis of large biological sequence data sets under the maximum likelihood criterion. PhD Dissertation, The University of Texas at Austin. Accepted.

Appendix 2.1. Character descriptions for morphological data used in phylogenetic analyses of *Phlaeopterus.* Most characters were developed by J.M. Campbell and modified by L. Mullen for these analyses. Characters 39 and 40 were modified from Moore and Legner (1979). Figure numbers are noted for character states that are illustrated.

1. *Size* (median habitus length): 0, less than 4.5-5.0mm (Fig. 2.1b); 1, 5.0-7.25 mm; 2, greater than 7.25 mm (Fig. 2.1a).

2. *Head width to length ratio*: 0, slightly narrower than long; 1, subequal; 2, greater than subequal but less than 4:3; 3, medium: width across eyes to length of head = 4:3; 4, broad: width across eyes to length of head = 5:4.

3. *Inner surface of mandible:* 0, with straight row of setae; 1, no setae; 2, with L-shaped row of setae.

4. *Molar area of mandible*: 0, with straight row of setae; 1, with no setae; 2, with L-shaped row of setae; 3, basal ridge with additional, oblique row of setae.

5. *Shape of labrum*: 0, 0.3-0.5 times as long as wide; 1, less than 0.3 times as long as wide.

6. *Dorsal surface of labrum*: 0, no micro-sensory pores; 1, sensory pores along anterior margin; 2, sensory pores across entire surface.

7. *Labial palpi*: 0, third palpomere at least twice as long as second segment; 1, third palpomere 1.6-1.8 times as long as second segement; 2, third palpomere 1.1-1.3 times as long as second segment.

8. *Interfacetal setae of eye*: 0, interfacetal setae on dorsal and ventral half; 1, interfacetal setae absent from dorsal half, with more than 10 setae on ventral half; 2, interfacetal setae absent from dorsal half, with 10 or fewer setae on ventral half.

9. *Base of epipharynx*: 0, with oblique, parallel rows of fine ridges; 1, smooth.

10. *Apical portion of epipharynx*: 0, with spines extending to apical margin; 1, smooth.

11. *Width of gula*: 0, less than 0.2 times as wide as mentum; 1, more than 0.2 times as wide as mentum.

12. *Width of lacinia*: 0, elongate and narrow; 1, broad.

13. *Maxillary palpi (length of fourth vs. third segment)*: 0, apical palpomere at least 4 times as long as third; 1, more elongate; second palpomere 2.4–3.9 times as long as third; 2, apical palpomere less than 2.3 times as long as third segment.

Appendix 2.1, continued.

14. *Maxillary palpi (length:width of third segment)*: 0, longer than wide; 1, not longer than wide.

15. *Hypopharynx*: 0, with rows of fine cilia; 1, lacking cilia.

16. *Antennal segments 5-10*: 0, 1.2-1.8 times as long as wide; 1, at least 2 times as long as wide.

17. *Sensory pits of antennae*: 0, absent; 1, present and with protrusions; 2, present and with pore-like openings.

18. *Interantennal groove*: 0, deeply depressed; 1, vague and shallowly depressed; 2, obsolete.

19. *Ocelli*: 0, present; 1, absent.

20. *Antocellar foveae (dorsal transverse impressions between eyes)*: 0, absent; 1, present.

21. *Nuchal constriction:* 0, distinct, post-ocular region clearly divided into temple and neck; 1, vague or slight with temples about 0.5 times width of eye; 2, vague or slight with temples less than 0.5 times as long as eye; 3, nuchal constriction indistinct.

22. Shape of lateral margins of pronotum: 0, strongly constricted basally; 1, widened basally (Figs. 2.9a, 2.9b); 2, evenly convex; 3, less widened basally.

23. *Pronotal punctation*: 0, punctures separated by distance slightly greater than diameter of one puncture; 1, punctures separated by distance equal to twice as great as diameter of puncture.

24. *Lateral edges of pronotal disk*: 0, nearly evenly convex; 1, explanate behind lateral foveae only; 2, broadly explanate posterior to lateral foveae but more narrowly explanate anterior to lateral foveae (Fig. 2.9b); 3, sides subequally explanate anterior and posterior to the lateral foveae (Fig. 2.9a).

25. *Pronotum (lateral foveae):* 0, with only trace of depression; 1, absent, apparently obscured by deflexed margin; 2, moderately depressed; 3, deeply depressed (Figs. 2.9a, 2.9b).

26. *Pronotal width*: 0, 1.4-1.6 times width of head; 1, narrower than 1.3 times width of head; 2, wider than 1.5 times width of head.

27. *Pronotal length:width:* 0, 0.70-0.79; 1, narrower than 0.70; 2, wider than 0.79 (Figs. 2.9a, 2.9b).

Appendix 2.1, continued.

28. *Pronotal maximum width vs. elytral width at base*: 0, distinctly less than combined elytral width; 1, subequal to combined elytral width.

29. *Elytra (humeral angles):* 0, convex, epipleural carina not projecting; 1, rectangular, epipleural carina projecting.

30. *Elytral (length vs pronotal length)*: 0, no more than 2 times as long as pronotum; 1, 2.1-2.2 times as long as pronotum; 2, 2.3-2.4 times longer than pronotum; 3, at least 2.5 times as long as pronotum.

31. *Elytra (apical margins):* 0, convex or subtruncate (Fig. 2.8b); 1, prolonged at suture (Figs. 2.8a, 2.8c).

32. *Wings*: 0, fully developed; 1, reduced (brachypterous); 2, absent (apterous); 3, nearly always fully developed, rarely reduced (brachypterous).

33. *Antemesoventral plate*: 0, large and differentiated; 1, reduced in size.

34. *Mesoventrite (tooth or lobe of anterior ridge):* 0, ridge with only a small lobe; 1, ridge with projecting tooth.

35. *Longitudinal mesoventral carina*: 0, present along midline; 1, reduced; 2, absent (obsolete) anterior to mesoventral ridge; 3, absent (obsolete) but mesoventrite with large median tubercle.

36. *Shape of tooth on mesoventral carina:* 1, tooth approximately evenly produced on anterior and posterior portion; 2, anterior margin of tooth much more strongly produced than posterior margin.

37. *Tooth on metatrochanter*: 0, lacking; 1, present.

38. *Glabrous portion of mesotibia*: 0, absent; 1, greater than length of basal tarsomere, less than or equal to basal two tarsomeres; 2, subequal to length of basal three tarsomeres (Fig. 2.10b); 3, usually nearly evenly pubescent to apices, sometimes with glabrous region less than length of basal tarsomere; 4, as long as basal four tarsomeres combined (Fig. 2.10a).

39. *Metatarsi (first segment)*: 0, as long as or longer than ultimate tarsomere; 1, shorter than ultimate tarsomere.

40. *Metatarsi (second tarsomere)*: 0, as long as first tarsomere; 1, shorter than first tarsomere.

41 *Wing-folding patches*: 0, on tergites IV and V; 1, on tergites IV, V and VI; 2, absent from all tergites.

Appendix 2.1, continued.

42. *Shape of wing-folding patches on tergite 5*: 0, round and widely separated; 1, broadly oval and narrowly separated; 2, combined into a single transverse band.

43. *Apical palisade fringe on tergite VII*: 0, present; 1, absent.

44. *Median lobe (carina)*: 0, not carinate (Fig. 2.11); 1, narrowly carinate; 2, apical carina relatively broad.

45. *Parameres vs. median lobe apex*: 0, parameres extending slightly beyond apex of median lobe; 1, parameres extending well beyond apex of median lobe.

46. *Internal sac (microspinules)*: 0, without or with few fine microspinules; 1, partially or completely covered with microspinules; 2, with patterns of larger sclerites.

Conclusion

In this thesis I have used the complementary methods of taxonomy and phylogenetics to uncover the evolutionary history of the rove beetle genus *Phlaeopterus*. In Chapter 1, I reviewed the taxonomic history of *Phlaeopterus*, synonymized and described species, provided a dichotomous key for the identification of species, and mapped the distribution of each species. Prior to this taxonomic revision, *Phlaeopterus* was comprised of 15 species. I described 8 new species, synonymized the monotypic genus *Vellica* with *Phlaeopterus*, transferred two species (*P. kootenayensis* and *P. stacesmithi*) to the genus *Unamis*, synonymized *P. rufitarsus* with *P. filicornis*, synonymized *P. brevipennis* and *P. longipalpus* with *P. cavicollis*, and demoted *P. cascadiensis* to a subspecies of *P. castaneus*, resulting in 18 *Phlaeopterus* species. I provided a diagnosis of the genus that includes 11 morphological characters, including characters of the mouthparts and male genitalia that have not been used in previous diagnoses.

In Chapter 2, I produced the first quantitative estimate of the phylogeny of *Phlaeopterus* using Bayesian and maximum likelihood methods with both morphological and molecular data. I analyzed the morphological and molecular datasets independently, in order to compare the resultant trees, as well as together in a comprehensive COI+morphology analysis. The combined COI+morphology phylogeny included *P. obsoletus*, the species lacking COI sequence data, which was otherwise missing from the COI-only phylogeny. I found strong support for the synonymy of the monotypic genus *Vellica* with *Phlaeopterus*, which is in agreement with the suggestion by Newton *et al*. (2000) that the two genera are not distinct. *Phlaeopterus castaneus* has two different COI haplotypes, one in the Cascade Range and one in the Rocky Mountains. The Rocky Mountain COI haplotype is

shared with *P. loganensis*, and suggests recent or ongoing hybridization between these two species in the region where their distributions overlap. This finding informed my decision to recognize two P. *castaneus* subspecies, *P. castaneus castaneus* and *P. castaneus cascadiensis*. These results speak to the value of incorporating both morphological and molecular data into taxonomic revision and phylogenetic analyses. The hybridization of *P. castaneus* and *P. loganensis* is not readily apparent from morphological or molecular data alone, and it is well documented that these two types of data can each compliment the weaknesses of the other (Hillis 1987, Hillis and Wiens 2000, Wiens 2004).

The unique snowfield and high-altitude stream habitat association of *Phlaeopterus* species puts these beetles at significant risk of extirpation, or even extinction, by a warming climate. Climate change-induced warming is occurring at high latitudes at a rate over twice the global average (Hansen *et al.* 2005), and high-altitude mountainous regions show even greater rates of warming (Rauscher *et al.* 2008). The snowfields in these regions, which act as traps for windblown invertebrates, are likely to decrease in size and abundance like the better-studied glaciers. Furthermore, insects and other invertebrates are particularly sensitive to changing climate (Hodkinson and Bird 1998). For example, a meltwater stonefly, *Lednia tumana* (Ricker 1952), which is endemic to alpine glacial meltwaters of Glacier International Peace Park, has been petitioned to be listed as endangered under the US Endangered Species Act due to climate change-induced loss of its glacial habitat (Muhlfeld *et al.* 2011, Jordan *et al*. 2016). The Cascade Range and surrounding mountains, one of the most *Phlaeopterus* species-rich regions, have seen drastic warming and reduction of snowpack (Belmecheri *et al*. 2015). I have assembled a large collection of *Phlaeopterus* museum specimens (over 11,000) from most major U.S. and Canadian insect

collections (n = 35). Based on this sample, *P. bakerensis* has not been collected since the late 1970's. *Phlaeopterus bakerensis* is known only from Mount Baker, Washington, where it is confined to the edges of snowfields at elevations of 1,220–1,700 m. This rare endemic is, to the best of my knowledge, the largest species in the entire subfamily Omaliinae, growing up to 10 mm in length. Another rare and highly endemic species described in Chapter 1, *P. olympicus,* is known only from the Olympic Mountains of Washington and was last collected in 1984. Since this time, multiple collection events by trained entomologists have yielded three other *Phlaeopterus* species (*P. fusconiger*, *P. cavicollis*, and *P. lagrandeuri*) from the Olympic Mountains, yet *P. olympicus* has not resurfaced. Similar trends can be seen in snowfield-associated beetles of the family Carabidae. A recently described carabid species, *Nebria praedicta* Kavanaugh and Schoville, (2009), occupies a similar ecological niche and is endemic to the Trinity Alps. The description of this species notes that the glacier that sustains the only known population of *N. praedicta* is receding and will likely soon disappear. The authors predict that continued warming will lead to the extinction of *N. praedicta* and another species, *Nebria turmaduodecima* Kavanaugh, 1981. A similar fate seems likely for some *Phlaeopterus* species, if they are not already extinct.

Literature Cited

Belmecheri, S., Babst, F., Wahl, E.R., Stahle, D.W. and Trouet, V., 2015. Multi-century evaluation of Sierra Nevada snowpack. *Nature Climate Change*, 6(1), 2-3.

Hansen, J., Nazarenko, L., Ruedy, R., Makiko, S., Willis, J., Del Genio, A., Koch, D., Lacis, A., Lo, K., Menon, S., Novakov, T., Perlwitz, J., Russell, G., Schmidt, G., Tausnev, N., 2005. Earth's energy imbalance: confirmation and implications. *Science*, 308(5727), 1431–1435.

Hillis, D.M., 1987. Molecular versus morphological approaches to systematics. *Annual review of Ecology and Systematics*, *18*(1), 23-42.

Hillis, D.M., and Wiens, J.J., 2000. Molecules versus morphology in systematics: conflicts, artifacts, and misconceptions. In 'Phylogenetic Analysis of Morphological Data'. (Ed. J. Wiens.) Smithsonian Institution Press: Washington, DC. pp. 1–19.

Hodkinson, I., Bird, J., 1998. Insect herbivores as sensors of climate in Arctic and host-specific change environments. *Arctic and Alpine Research*, 30(1), 78–83.

Jordan, S., Giersch, J.J., Muhlfeld, C.C., Hotaling, S., Fanning, L., Tappenbeck, T.H. and Luikart, G. 2016. Loss of genetic diversity and increased subdivision in an endemic alpine stonefly threatened by climate change. PloS one 11(6): e0157386.

Kavanaugh, D.H., 1981. *Studies on the Nebriini (Coleoptera: Carabidae), IV. Four new Nebria taxa from western North America* (No. 59 CAL). California Academy of Sciences.

Kavanaugh, D.H., Schoville, S., 2009. A New and Endemic Species of *Nebria* Latreille (Insecta: Coleoptera: Carabidae: Nebriini), Threatened by Climate Change in the Trinity Alps of Northern California. *Proceedings of the California Academy of Sciences*. 60(7), 73–84.

Muhlfeld, C.C., Giersch, J.J., Hauer, F.R., Pederson, G.T., Luikart, G., Peterson, D.P., Downs, C.C., Fagre, D.B., 2011. Climate change links fate of glaciers and an endemic alpine invertebrate. *Climate Change* 106, 337–345.

Newton, A.F., Thayer, M.K., Ashe, J.S., Chandler, D.S., 2000. 22. Staphylinidae Latreille, 1802. *In: Arnett, R.H. & Thomas, M.C. (Ed.), American Beetles, Vol. 1. Archostemata, Myxophaga, Adephaga, Polyphaga: Staphyliniformia*, 272–418.

Rauscher, S.A., Pal, J.S., Diffenbaugh, N.S., & Benedetti, M.M., 2008. Future changes in snowmelt-driven runoff timing over the western US. *Geophysical Research Letters*, 35(16), L16703.

Ricker, W.E., 1952. Systematic studies of Plecoptera. Indiana University Publishing Science Services, 18, 1–200.

Wiens, J.J., 2004. The role of morphological data in phylogeny reconstruction. *Systematic Biology*, 53(4), 653–61.